

# Science Progress.

---

No. 3.

MAY, 1894.

Vol. I.

---

## THE DETERMINATION OF THE AVAILABLE PLANT FOOD IN SOILS.

THE chemical analysis of a soil, if carried out with completeness and real accuracy, is a work demanding much labour and skill. It has been frequently regarded as a thankless task. Agricultural chemists of high standing have proclaimed that such analyses were unreliable, because it was improbable that the very small quantity of soil investigated by the chemist could fairly represent the enormous quantity contained in a field. They further pointed out that the results afforded no information upon the most important questions. There was frequently nothing to show why one field was fertile and another not. The quantities of plant food shown by the analysis were generally, when calculated on an acre of soil, extremely large; yet experience had probably taught the farmer that the application of a small quantity of a soluble phosphate, of a potassium salt, or of a nitrate, had the effect of considerably increasing the crop. Some analysts, like Prof. Hilgard, have continued patiently at work, notwithstanding hostile criticism, and by the accumulation of experience have become able to interpret soil analyses with considerable success, especially if relating to a district already investigated. In such cases the agricultural meaning of the analysis did not lie on its surface, but was elucidated by bringing the analytical

results into connection with other previously ascertained facts.

The main object of a chemical analysis is clearly to show what is the quantity of plant food existing in the soil. Physiologists are aware that the plant food in a soil occurs in two distinct forms. A plant can, in the first place, feed upon substances which are in solution. The water in a soil contains a more or less considerable amount of carbonic acid, and in this weak solution of carbonic acid certain of the ingredients of the soil are soluble. Soil water generally contains a good deal of calcium and magnesium carbonate; it contains nitrates, chlorides, and sulphates, with soluble silicic acid. It generally contains no phosphates, and only traces of potassium salts; sodium salts may, however, be present. If, therefore, the plant were entirely dependent on the soil solution for its nourishment, it would be starved, as two essential constituents of plant food, phosphates and potash, are not supplied by this medium.

The second mode in which a plant feeds is by the solvent action of its roots. This extremely important function of the roots has been far too little investigated. Sachs was the first to show that the root hairs of certain plants had the power of eroding polished plates of marble, dolomite, and osteolite, by virtue of the acid sap which they contained. Zöller, more than thirty years ago, ascertained at Liebig's suggestion that calcium phosphate, ammonium-magnesium phosphate, and the potash of a freshly-manured soil, were dissolved when placed on a membrane the other side of which was in contact with a weak solution of hydrochloric, acetic, or citric acid. It is generally, and probably correctly held, that this solvent action of the roots is especially effective towards the phosphoric acid, potash and other substances which have been previously absorbed by the soil from solution, and which are thus held on the surface of the soil particles. As to the nature or amount of the free acid present in root sap little is definitely known. A. Mayer lays most stress on the presence of oxalic acid, which he found in several instances.

The importance of this solvent action of the roots can

hardly be over-rated. Most of the phosphoric acid in soil exists as a basic ferric phosphate, insoluble in water and in carbonic or acetic acid, and but for the existence of this solvent power in roots would remain useless to vegetation. The potash, and we may add the ammonia, of soils is held in almost equally insoluble combinations; but analytical chemists are aware that the whole of the ammonia, and more or less of the potash, becomes soluble as soon as the soil is placed in a weak solution of hydrochloric or nitric acid. The acid sap of the roots is thus equally required to bring about the solution of these important soil constituents.

It is clear from what has been now said that it should be the aim of a soil analysis to show what is the amount of soluble plant food which a soil contains; soluble, that is, either in water, or in the acid root sap of the crops. Only when this is done can the present fertility of a soil be plainly indicated by its analysis.

There is no difficulty in ascertaining the amount of plant food soluble in water. By following Schloesing's plan, and displacing, by means of water, the solution actually present in the soil, we can, if we please, examine the natural solution in the soil. Or by extracting a powdered soil with water on a vacuum filter, we may speedily remove the whole of the freely soluble salts, including nitrates and chlorides. This mode of proceeding will suffice to show what is the amount of immediately available nitrogen which a soil contains, as this will be represented by the nitric nitrogen found on analysis. The following example, taken from the series of analyses made of the soils of the Rothamsted barley field in March, 1882, will show the enormous differences between the quantity of the total nitrogen of the soil and the effective nitrogen existing as nitrates, and also the dependence of fertility upon the latter.

NITROGEN IN ROTHAMSTED BARLEY SOILS, MARCH, 1882,  
IN POUNDS PER ACRE.

Plot.	Total Nitrogen First 9 Inches of Soil.	NITRIC NITROGEN.			Barley Crop, 1882 (Grain).
		First 9 Inches of Soil.	27 Inches of Soil.	Afterwards added as Ammonia.	
	Lbs.	Lbs.	Lbs.	Lbs.	Bushels.
2 O	2275	6'4	18'4	None	21 $\frac{7}{8}$
2 A	2578	7'4	27'1	43'0	45 $\frac{1}{4}$

The two plots here selected as illustrations had both grown barley for thirty years, and had both received every year a dressing of superphosphate. The only difference between them was that while plot 2 O had received no nitrogenous manure, plot 2 A had received ammonium salts every year, supplying forty-three lbs. of nitrogen per acre. The difference in fertility of the two soils is seen to be very great, the soil receiving ammonia giving more than twice as large a produce as the soil without nitrogenous manure. Yet the soil without nitrogenous manure contained 2275 lbs. of nitrogen in the first nine inches of soil, which yet could only produce twenty-one and seven-eighth bushels of barley. The soil with nitrogenous manure contained 2578 lbs. of nitrogen in the first nine inches. Had the produce in this case been in proportion to the total nitrogen in the soil and manure, it should have yielded about twenty-five bushels of barley. The actual produce of forty-five and a quarter bushels obtained is clearly due to the much larger amount of nitric nitrogen present on plot 2 A. The ratio of the total nitrogen on the two plots is indeed 100 : 115. The ratio of the nitric nitrogen (assuming that the whole of the ammonia nitrified) is 100 : 381. The ratio of the crops (corn only), 100 : 207.

Although the determination of nitric nitrogen in a soil is an excellent means of ascertaining the amount of effective nitrogen which it contains, the method is of little use to the agricultural analyst. If the determination is to represent the condition of the soil in the field, the analysis must be



made immediately the sample has been taken, or the soil must be at once dried with suitable precautions (*Trans. Chem. Soc.*, 1882, 351). Even, however, when this is done, the results obtained will fail to indicate the intrinsic quality of the soil, as the amount of nitrate present at any moment is largely influenced by the character of the preceding weather, and by the cropped or uncropped condition of the land. Much better results would be obtained if the analyst were to ascertain what was the rate of nitrification in the soil under certain fixed conditions. These rates would at once indicate grades of fertility, and the accumulation of results would soon enable the analyst to associate them with a definite fertility of the soil.

We have spoken of the plant food taken up from ready formed solutions in the soil : we turn next to the undissolved plant food of the soil brought into solution by contact with the acid surfaces of the root hairs. If the analyst is to form any idea of the quantity of effective phosphoric acid or potash which a soil contains, he must employ some solvent which shall imitate the solvent action of the root hairs. In approaching such a problem we are at once confronted with many difficulties. We do not fully know the composition of the root sap of any plant, and there can be no doubt but that the sap of different plants differs very materially in composition, and that to this very cause is due some of the remarkable differences in the capacity of various plants to supply themselves with food from the soil.

Dr. Bernard Dyer has recently published (*Trans. Chem. Soc.*, 1894, 115) determinations of the acidity of root sap in one hundred and three plants, representing twenty natural orders.

A summary of his results is given in the following table :—

## ACIDITY OF THE ROOT SAP OF PLANTS (DYER).

Orders.	Specimens examined.	Acidity of Root Sap reckoned as Citric Acid.	
		Mean.	Extremes.
		Per Cent.	Per Cent.
Rosaceæ . .	4	3'40	1'86—5'53
Plumbaginææ .	2	2'19	2'03—2'34
Onagraceæ . .	2	2'04	1'97—2'10
Ranunculaceæ .	2	1'13	1'11—1'14
Boraginaceæ . .	1	1'00	—
Caryophyllaceæ .	4	0'89	0'80—1'14
Araliaceæ . .	2	0'88	0'70—1'05
Leguminosæ . .	9	0'88	0'34—1'55
Cruciferae . .	25	0'80	0'37—1'42
Scrophulariaceæ .	3	0'73	0'47—1'16
Primulaceæ . .	2	0'68	0'63—0'73
Umbelliferae . .	5	0'67	0'33—1'10
Compositæ . .	4	0'63	0'46—0'76
Campanulaceæ . .	2	0'62	0'55—0'68
Gramineæ . .	20	0'62	0'28—1'06
Tropæolaceæ . .	1	0'57	—
Chenopodiaceæ . .	8	0'52	0'25—0'70
Dipsaceæ . .	2	0'44	—
Liliaceæ . .	4	0'36	0'17—0'62
Solanaceæ . .	1	0'34	—

The mean acidity of the 103 determinations of root sap is 0'85 per cent., reckoned as crystallised citric acid; and the mean acidity of the twenty orders is 0'91 per cent. When we look, however, at the agricultural crops, we find the acidity less, the mean acidity of the Leguminosæ, Cruciferae, Gramineæ, Chenopodiaceæ and Solanaceæ being 0'63 per cent.

The difficulty of determining exactly the effective acidity of the sap present in the root hairs is very great, and the results of the numerous experiments just quoted are naturally only approximate. Nor does Dr. Dyer assume that the acid present is necessarily citric acid; the results are given in terms of this acid for a reason which will presently appear.

It has been recognised by many agricultural chemists that we should obtain a much more correct idea of the

available plant food in a soil if the extraction of the soil were made with a weak instead of a strong acid. More than twenty years ago dilute acetic acid was used by E. Peters; and dilute acetic acid, and dilute nitric acid, by Hermann von Liebig.

If the object is to determine the available potash, it probably does not matter what acid is employed. Schloësing has taught us that if a soil is diffused in water, and small quantities of hydrochloric or nitric acid are gradually added till the bases in the soil are satisfied, and the solution remains permanently and distinctly acid, that the whole of the ammonia, and the whole of the potash *held in the same way* as the ammonia, will come into solution. The potash thus dissolved, Schloësing teaches, is the potash which is available to plants, and this opinion is probably correct.

If, however, the object is to determine the amount of available phosphoric acid which the soil contains, the nature of the acid becomes important. The phosphoric acid of non-calcareous soils exists principally as a basic ferric, or possibly aluminic, phosphate; such compounds are not dissolved by acetic acid, which yet is quite capable of dissolving precipitated calcium phosphate. Dehérain and Vogel have proposed to use acetic acid as a means for determining whether a soil stood in need of phosphatic manure, and upon calcareous soils the amount of phosphoric acid soluble in acetic acid is probably an indication of practical importance. It is well known, however, that non-calcareous soils often contain a large quantity of available phosphoric acid, although the existence of this is not shown by extraction with acetic acid.

The comparative action of various acids upon the phosphates contained in soil has been scarcely studied. Much attention has, however, been given to the determination of the available insoluble phosphates in manures, the reagent usually employed for this purpose being ammonium citrate, or, more rarely, citric acid, or a mixture of the two. Ammonium citrate is an excellent solvent for ferric or aluminic phosphate, and a less efficient solvent for calcium phosphate, unless this occurs in a precipitated condition. A weak

solution of citric acid is, on the other hand, a far better solvent of calcium phosphate in all its forms, and a worse solvent of ferric and aluminic phosphate.

A solution of ammonium citrate has been employed by Petermann for many years to indicate the proportion of available phosphoric acid in a soil; or, as he expresses it, to distinguish between the phosphates belonging to the original rock, and the phosphates belonging to the residues of previous manuring. Petermann finds that in well-manured sandy soils or loams, from twenty-five to eighty per cent. of the total phosphoric acid is soluble in alkaline ammonium citrate; while in schists and greywackes, only a few per cent. of the total phosphoric acid are thus soluble. Generally a larger proportion of the phosphoric acid is soluble in ammonium citrate in the case of arable than of virgin soils.

Dr. Dyer describes experiments of his own in which two soils were treated with ammonium citrate solutions of various strengths, one of the soils being also treated with various strengths of a solution of free citric acid. The results show that the amount of phosphoric acid dissolved by ammonium citrate increases with each increase in the strength of the reagent; the rate of increase of the dissolved phosphate diminishes, however, rapidly when considerable concentrations of the solvent are reached. The amount of potash dissolved remains, on the other hand, nearly constant after a certain considerable strength of the ammonium citrate has been attained. The amount of phosphate dissolved by the free citric acid, in the case of the single soil experimented on, increases largely with an increase in the strength of the acid, and the amount dissolved by the greatest concentration of acid (five per cent.) was more than three times as great as that dissolved by a fifty per cent. solution of ammonium citrate. No experiments are recorded as to the effect of an increase in the strength of the citric acid on the amount of potash dissolved.

Dr. Dyer has chosen a one per cent. solution of citric acid as the reagent for extracting soils, with the view of determining the amount of "available mineral plant food" which they contain. That extraction with such a solution

must yield results much more nearly representing the solvent action of plant roots than are obtained when the soil is extracted with concentrated hydrochloric acid, may be freely granted, but it is perhaps open to doubt whether the solution is the best which could be employed. Actual experiments can alone decide such a question. We may, however, remark that the strength of citric acid adopted is distinctly greater than the total acidity found in the root sap of agricultural crops. We would also point out that plant sap must contain combined as well as free organic acids, and the fact that bases are dissolved out of the soil by the action of this sap shows that a supply of combined acid is constantly maintained. Now we have just seen that the action of a soluble citrate (or, at all events, of ammonium citrate) upon ferric and aluminic phosphate, and upon calcium phosphate, is quite distinct from the action of free citric acid, the citric acid especially attacking the calcium phosphate, while the citrate had a preponderating action upon the ferric and aluminic phosphates. It is thus open to doubt whether the selection of free citric acid only, is perfectly judicious. In this connection it may be mentioned that P. Wagner, in 1886, proposed the use of a solution containing 0·2 per cent. of free citric acid, with 3·0 per cent. of citric acid combined with ammonia, for the purpose of ascertaining what proportion of the phosphate of a manure was to be reckoned as immediately available for plants; and he was led to adopt this proportion of free and combined acid because it gave the same results as to the comparative value of manures as were shown by actual experiments with agricultural plants.

We now turn to the results obtained by Dr. Dyer by the use of a one per cent. solution of citric acid. These results are of great interest. He has worked on a special series of soil samples taken from twenty-two plots in the barley field at Rothamsted in the autumn of 1889, and representing the first nine inches in depth. In these samples he has determined both the total phosphoric acid and potash, and also the phosphoric acid and potash extracted by a one per cent. solution of citric acid.

As an example of the immense difference to the crop

which is occasioned by a difference in the solubility of the phosphates in the soil, we will take the results relating to plots 1 A and 2 A.

PHOSPHORIC ACID IN ROTHAMSTED BARLEY SOILS, 1889,  
IN POUNDS PER ACRE IN FIRST NINE INCHES.

Plots.	Total Phosphoric Acid.	Phosphoric Acid soluble in 1 per cent. Citric Acid.	Barley Crop, 1889 (Grain).
	Lbs.	Lbs.	Bushels.
1 A	2452	152	22 $\frac{1}{2}$
2 A	4373	1073	35 $\frac{1}{4}$

These two plots have grown barley continuously for thirty-eight years, and during the whole of this time both have received every year the same quantity of ammonium salts. Plot 2 A has also received every year three and a half cwts. of superphosphate per acre; while during the whole time no phosphates have been applied to 1 A.

On plot 1 A, where the barley has been grown for so many years without any supply of phosphates, the want of phosphates is keenly felt, the average produce being about thirteen bushels less than where phosphates are supplied. It appears by the figures in the above table that plot 1 A still contains 2452 lbs. of phosphoric acid in the first nine inches of soil (0.097 per cent. of the dry soil); and yet it is evident, by comparison with the results on 2 A, that the addition of sixty-four lbs. of phosphoric acid (three and a half cwts. of superphosphate) as manure would greatly increase the produce. The reason of the small availability of the phosphates in this soil is revealed when we look at the amount dissolved by dilute citric acid: out of the 2452 lbs. only 152 lbs. are soluble in this reagent.

On plot 2 A, it appears from the figures in the table that a large accumulation of phosphoric acid remains from the thirty-eight annual dressings of superphosphate which have been applied; and, further, that more than half of this accumulated phosphoric acid, or 1073 lbs., still remains in a

condition soluble in dilute citric acid. The last-named fact is one of much practical importance.

The great difference between the supply of phosphoric acid on plots 1 A and 2 A is thus plainly shown by the analyses, and most conspicuously by the results obtained on extraction with dilute citric acid.

The facts just mentioned must suffice as an example of the results obtained by the application of Dr. Dyer's method to soils known to be respectively poor and rich in available phosphoric acid; we will next give an example of the results he has obtained in his determinations of potash.

POTASH IN ROTHAMSTED BARLEY SOILS, 1889,  
IN POUNDS PER ACRE IN FIRST NINE INCHES.

Plots.	Total Potash.	Potash soluble in 1 per cent. Citric Acid.	Barley Crop, 1889 (Straw).
	Lbs.	Lbs.	Cwts.
2 A	36,376	57	18 $\frac{1}{4}$
4 A	43,301	753	21 $\frac{1}{4}$

Plots 2 A and 4 A have each received during thirty-eight years the same annual dressing of ammonium salts and superphosphate, but 4 A has received in addition throughout the whole period a mixture of potassium, sodium, and magnesium sulphate. For many years the want of potash was not felt on plot 2 A, although none was applied, but in later years a falling off in the quantity of straw has become apparent, as will be seen in the above table; moreover, the composition of the ash of the straw shows that very little potash is at the disposal of the crop on this plot. Notwithstanding, therefore, that the soil still contains the enormous quantity of 36,376 lbs. of potash in the first nine inches (1.439 per cent. of the dry soil), exhaustion of available potash has clearly commenced, and we find accordingly that the treatment with a one per cent. solution of citric acid only succeeds in dissolving fifty-seven lbs. of potash. This is certainly a most striking result.



The same soil treated for a short time with strong hydrochloric acid yielded potash equal to 6269 lbs. per acre.

Plot 4 A has received during the thirty-eight years about 4100 lbs. of potash per acre as manure; the total potash of the two plots mentioned in the table differs, however, by more than this amount, probably from some inaccuracy in sampling the soils. On the plot manured with potash there are found 753 lbs. of potash soluble in one per cent. citric acid. This result is in striking contrast with the 57 lbs. yielded by the plot in which potash exhaustion has commenced. The proportion of the potash manure remaining soluble in citric acid, and therefore apparently still available to the crop, is however far smaller than the proportion of phosphoric acid remaining available in the experiments already described. The cause of this requires further investigation. We must either assume that the potash has entered into combinations which are not decomposed by the weak citric acid, or that it has passed into the subsoil.

The examples quoted sufficiently show that the quantities of phosphoric acid and potash extracted from these heavy loams by a one per cent. solution of citric acid are plainly related to the quantities of *available* phosphoric acid and potash present, as shown by the barley crops grown on the land. When, however, we look a little more nearly at the figures yielded by the treatment with citric acid, we see quite plainly that the action of this acid by no means exactly represents the action of the barley roots; that, in fact, the one per cent. solution of citric acid is a much better solvent for soil phosphates than it is for soil potash. If we take the mean of Dr. Dyer's determinations of phosphoric acid in eight plots of the barley field, to which no phosphates had been applied for thirty-eight years, we find 199 lbs. per acre as soluble in one per cent. citric acid. On all these plots the crop was greatly reduced from the deficiency of available phosphoric acid in the soil. If we now take the mean of the determinations of potash in eight plots to which no potash had been applied, we find 98 lbs. per acre soluble in the one per cent. solution of citric acid. Yet this far smaller amount

of potash was generally sufficient for the barley crop, a lack of potash being only shown in some instances by a deficiency in the straw.<sup>1</sup>

It is thus evident that, compared with the one per cent. citric acid, the barley roots took up potash from the soil much more easily than they took phosphoric acid; or, in other words, that if the action of the citric acid is to be made comparable with that of the barley roots, its solvent powers for soil phosphates must be reduced. We have already seen that the average acidity of root sap in the *Gramineæ* was found by Dr. Dyer to be equal to 0.62 per cent. of citric acid. In the single specimen of barley root sap examined by him the acidity was only 0.38 per cent. If Schlœsing's view be correct, and it suffices merely to acidify the soil in order to bring the available potash into solution, a reduction in the strength of the citric acid might be made without diminishing the quantity of potash dissolved, while it would probably considerably diminish the quantity of phosphates brought into solution.

As Dr. Dyer is continuing his researches, and has command of the best series of soils which is available for the establishment of a method of determining the amount of effective plant food in soils, we may be permitted perhaps to point out some of the questions which seem at the present time to stand in need of answers.

Dr. Dyer has worked upon undried soils. It is very important that we should know if the citric acid method yields the same results before and after the soil is dried. Unless a soil can be dried sufficiently to admit of powdering and sifting, it is impossible to obtain a fair sample of it for analysis, and thus a method which demands undried soil becomes of little practical use.

<sup>1</sup> Dr. Dyer's explanation of the relatively low proportion of soluble potash found in the soils from the fact that the soil samples were taken in autumn, before the winter weathering had taken place, seems untenable. The quantities of potash and phosphoric acid found in autumn must be those existing in the previous spring, that is, after winter weathering, minus that removed in the crop. The quantity removed in the preceding crop is thus the only correction which need be applied in the case of autumn sampling, and this correction must affect both the phosphoric acid and potash.

Can the method proposed be applied to soils containing variable amounts of calcium carbonate, which will of course neutralise the citric acid? If calcium carbonate is mixed with a soil, of which the composition by the citric method is already known, can the former result be again obtained by extracting it with citric acid?

What is the solvent action on phosphates and potash of citric acid of strengths below one per cent. when working on a poor and rich Rothamsted soil? Is the action of the citric acid modified by the presence of calcium citrate in solution?

For the further elucidation of the subject it is important that some typical soils should be extracted with acetic acid, and with ammonium citrate, as well as with citric acid.

There are a number of very interesting and important facts in Dr. Dyer's paper which we cannot now call attention to as they do not belong to our present subject. We must not, however, end the present paper without referring to the entirely different view as to the condition of the available plant food in soil which has been proposed by L. Grandeau.

Grandeau was led by his investigations to believe that the effective mineral plant food in a soil was always in combination with humic matter, and that this humic matter was the indispensable vehicle necessary to transfer this mineral food to a growing plant. Fertile soils, he said, offer their mineral ingredients to plants in a state similar to that in which they are contained in farmyard manure. His plan of analysis was first to subject the soil to a preliminary extraction with very dilute hydrochloric acid to decompose the humates and remove basic matter, and then to extract the residual soil with ammonia. The dark-coloured solution thus obtained was evaporated to dryness, the residue ignited, and the mineral matter left was determined by ordinary methods of analysis.

Grandeau's method has been submitted to a careful study by O. Pitsch (*Landw. Versuchs. Stat.*, xxvi., 1). Having examined many soils by this method, but apparently chiefly with regard to their richness in phosphoric

acid, he concludes that in the case of sandy loam and peaty soils, the method affords a much better criterion of their fertility than is afforded by extracting the soil with strong acids; but that in the case of clay soils, the ammonia-soluble phosphoric acid is by no means a measure of the soil's fertility. He gives a few complete analyses of the mineral matter extracted by ammonia. All the essential constituents of plant food are present. Ferric and aluminic phosphate form about half of the ash, and silica is a large constituent; on the other hand, the bases—potash, lime and magnesia—are present only in small quantity.

Pitsch entirely disagrees with Grandeau's fundamental proposition that the substances extracted by ammonia are all combined with humus in the soil, and are taken up by plants solely from such combinations. He believes that the ferric and aluminic phosphate found in the ammonia solution have been extracted from the soil in the course of the analysis owing to their solubility in ammonium humate. He prepared ammonium humate, and compared its solvent action on various phosphates with that of alkaline ammonium citrate, and found that the solvent power of the humate exceeded that of the citrate both in the case of tricalcic phosphate and ferric phosphate. The *rationale* of the method is thus explained: if the soil contains a sufficient amount of humic matter, the extraction with ammonia becomes a similar proceeding to the extraction of a soil with ammonium citrate. The facts brought to light by these investigations appear to indicate that soluble humates have a special solvent power for phosphates; and, if this be the case, soils well supplied with humus, or manured with farm-yard manure, will generally also be well supplied with available phosphoric acid, and a part of Grandeau's contention will be substantiated. It would be interesting to know how a few typical Rothamsted soils behave when treated by Grandeau's method.

R. WARINGTON.

## THE EMBRYOLOGY OF THE PORIFERA.

IN few groups of the animal kingdom has the true nature of the embryonic development been so little understood, or the statements of the investigators of this subject so contradictory, as in sponges. An attempt to reduce their ontogeny to a common type was made by Haeckel, who wished to fit them in with his Gastræa theory, and under the influence of this idea regarded all sponge larvæ as gastrulæ; in fact he even went so far as to depict the larvæ of *Ascetta primordialis* and other species as free swimming gastrulæ of a most typical kind.<sup>1</sup> It was soon shown, however, by the more accurate studies of Schmidt, Metschnikoff and Schulze on the embryology of Calcarea that Haeckel's figures and descriptions were far from being true to nature, and that the larvæ of Ascons could in no way be regarded as gastrulæ, while the process of invagination undergone by the Sycon larvæ was in some respects the reverse of a typical gastrulation.

By the careful investigations of Schulze and Metschnikoff on the development of *Sycandra*, the ontogeny of this form became better known than that of any other sponge, and a distinct type of development was established, characterised by an *amphiblastula* larva, composed half of columnar ciliated cells, half of granular, rounded, non-ciliated cells. This larva was found to be characteristic of Sycons and Leucons generally, and also of *Ascandra* among Ascons. It is thus more or less universal among Calcarea, with the exception of the most primitive forms (*Ascetta*). The most striking feature of this type of development is that the ciliated cells become invaginated into, or overgrown by, the granular non-ciliated cells, and that the former cells give rise to the collar-cell layer

<sup>1</sup> Die Kalkschwämme, 1872; compare also *Natürliche Schöpfungsgeschichte*, fifth edition, Berlin, 1874, pp. 454 *et seq.*, taf. xvi.

of the adult, as well as probably to the lining of the gastral cavity; in short, that the ciliated cells of the amphiblastula become the future "endoderm," and not, as had been assumed before, the ectoderm. On the other hand, the cells in the amphiblastula larva, which become the ectoderm of the adult sponge, are those cells which are laden with the food yolk of the ovum, the reverse of what usually occurs in the development of other types of animals; for, as a general rule, food yolk, if present, is contained in cells of the endoderm. These anomalies in development did not receive an explanation, as might have been hoped, by comparison with the lowest calcareous sponges (*Ascetta*); for in the latter a mode of development occurred which apparently differed widely from the amphiblastula type, though, as we shall see later, the difference is probably not so great as it seems.

While the course of development in calcareous sponges, and especially in the amphiblastula type, was thus made out more or less clearly, even if it appeared somewhat strange when compared with the development of Metazoa other than sponges, the embryology of siliceous sponges, on the other hand, remained very imperfectly understood until quite recently. The typical larva of Silicispongiæ was shown by all the investigators to be a solid organism, consisting of a superficial layer of ciliated cells enclosing an internal mass of granular cells. The ciliated layer sometimes completely enclosed the granular cells, and sometimes left them uncovered at one of the poles. In the latter case a comparison with the amphiblastula of *Calcarea* seemed obvious,<sup>1</sup> but was negatived by the fact, in which all investigators were agreed, that the ciliated cells of the embryo gave rise to the ectoderm of the adult, while the collar-cell layer arose from the granular inner mass of the larva, the exact reverse of what occurs in the amphiblastula type. It is true that in the larva of *Spongilla* Götte described the ciliated cell layer

<sup>1</sup> Such a comparison was made by Metschnikoff (*Zeitschr. f. wiss. Zool.*, xxiv., 1874, p. 12) and by Balfour (*Comparative Embryology*, vol. i., p. 147).

of the larva as being thrown off, and the whole sponge as arising from its inner mass, but this statement, now known to be erroneous, did not serve to put things in any clearer light. With regard to other facts in the metamorphosis of the larva of Silicispongiæ the statements of investigators were very contradictory. Some authors described the fixation as taking place by the non-ciliated pole, which was regarded as the blastopore, and the whole larva was then compared to the *amphigastrula* or invaginated stage of Sycons, which had been clearly shown to fix itself by the blastopore or orifice of invagination. But, according to other authors, again the fixation of the larva took place by the ciliated pole, and with regard to other details of the metamorphosis the statements were equally at variance. Moreover, certain of the lower forms such as *Oscarella*, *Halisarca* and *Plakina* were shown to have a type of development very different from that prevailing in Silicispongiæ, and more resembling the process known to occur in Ascons.

It was therefore impossible, in the face of such differences in the mode of development, to reduce the embryology of sponges to any uniform scheme or fundamental type. The most that could be said with certainty was that all sponges had a free swimming larva with the surface formed either completely or partially of a layer of flagellated cells, and that the larva soon became fixed and developed into a young sponge. This larva more or less resembled the planula larva of Cœlenterates, in which the outer ciliated covering becomes the adult ectoderm, and in a similar manner the ciliated cells of sponge larvæ were said in nearly every case to become the adult ectoderm. But in one type, and that too the best known, namely, the *amphiblastula*, it was shown beyond all doubt that the ciliated cells became the *endoderm*; that is to say, they developed into the layer of collared cells, which most zoologists were agreed in comparing with the endoderm proper of Cœlenterata. This fact separated the amphiblastula larva from all other known sponge or Metazoan larvæ, and made it, in particular, impossible to compare the amphiblastula with



the larva it most nearly resembled, namely, the partially ciliated larva of *Silicispongiæ*; for the cell layers which resembled each other in appearance and position in the two types of larvæ were apparently precisely opposite in their homology.

With matters in this condition, an entirely new light has been thrown upon the question by the independent investigations of Maas in Germany, and Yves Delage in France. These two authors, though differing greatly in details, are agreed upon certain fundamentally important points, namely, that in the solid, planula-like larva of siliceous and horny sponges, the flagellated external cell layer, contrary to former statements, gives rise to the collar cells of the chambers of the adult sponge, while the inner mass of cells gives rise to the flattened epithelium lining the outer surface and the canal system, as well as to the whole of the so-called mesoderm of the sponge. Or, to put it differently, if we agree to term the collar-cell layer of an adult Ascon, or any other sponge, the *endoderm*, its flattened epithelium *ectoderm*, and the intermediate layer *mesoderm*; then, in the larva of siliceous sponges, the flagellated cell layer is, as in the amphiblastula of *Calcarea*, the endoderm, while the inner mass of granular cells represents an ecto-mesoderm. We thus find a fundamental *agreement*, instead of difference, between the type of larva, most common in calcareous, and siliceous sponges respectively. On the other hand, the apparently paradoxical fact of endoderm completely or partially surrounding ectoderm, separates them completely from other Metazoan, and especially from Cœlenterate larvæ, and for this reason it will be best to avoid at the outset such terms as ectoderm and endoderm, as more or less implying homologies outside the group, and to consider simply the plain facts of development, as stated by Maas and Yves Delage.

The investigations of Maas commence with the segmentation of the egg and extend over the larval life and metamorphosis up to the young sponge, while Delage has studied the post-larval development only. The species studied by Maas are *Esperia* (*Esperella*) *Lorenzi* O. S. and

*E. ligua*, Bwk. (metamorphosis), *Axinella Crista-galli* n.sp. (metamorphosis), *Myxilla rosacea* O. S. (from the egg), *Gellius varius*, Bwk. (metamorphosis), and *Chalinula fertilis*, Keller (from the egg), and a few observations are detailed upon the larvæ of some other species and the development of *Euspongia officinalis*, *Hircinia variabilis*, and *Spongilla*.<sup>1</sup> Delage has investigated the metamorphosis of *Spongilla fluviatilis*, Lbkhn., *Esperella sordida*, Bwk., *Reniera densa*, Bwk., and *Aplysilla sulfurea*, F. E. S.

According to Maas the segmentation is more or less uniform in all the species. The first two cleavages run meridionally and at right angles to one another, and divide the egg into four equal segments. The third furrow is equatorial and separates the ovum into four smaller and four larger blastomeres, an inequality which is maintained from this stage onwards. A segmentation cavity, virtually present at the eight-cell stage, is more distinct in the later stages, especially when the inequality in the blastomeres is more pronounced. In other cases it is less distinct, and may become obliterated by blastomeres pressing into the interior. The embryo soon becomes distinctly two-layered, owing to the more rapid division of the peripheral cells. At first the cells at one pole are smaller than those at the other, but later the embryo becomes surrounded by the smaller cells and then consists of two distinct layers: (1) a peripheral layer of small cells, with clear protoplasm and small, deeply staining nuclei filled with a close framework of chromatin; (2) an inner mass of larger cells, filled with coarse granules (yolk) and containing each a vesicular nucleus with nucleolus. In *Chalinula* and *Myxilla* the layer of smaller cells is only one or two cells deep and does not completely envelop the inner mass, but leaves the latter exposed at one pole. In *Hircinia*, however, the inner mass is completely covered, the layer

<sup>1</sup>In his former paper on the development of *Spongilla* (*Zeitschr. f. wiss. Zool.*, bd. 1., 1890) Maas gave a very different account to that which he now believes to be correct. He then described the ectoderm of the adult sponge as arising from the ciliated cells of the larva.

of small cells being largely developed and three or four cells deep all round.

The embryo at the later stages of segmentation has a striking resemblance to the cases of unequal segmentation, followed by epibolic gastrulation, which are of such common occurrence in other groups of animals. In fact, were it not for the subsequent fate of the two kinds of cells, we should have no hesitation in identifying, by analogy with other Metazoa, the micromeres as ectoderm cells, and the large, granular yolk containing cells as endoderm. But, as a matter of fact, the micromeres give rise to the ciliated cells of the larva and the collar cells of the adult, while the macromeres become the inner mass of the larva and the flattened epithelium and mesoderm so called of the adult.

The next step is the histological differentiation of the cells composing the two layers which hitherto have had the appearance of blastomeres. At the same time that the first spicules appear in the interior of the embryo, the cells of the peripheral layer begin to arrange themselves to form an epithelium, composed of cells which are first rounded, then cubical, then columnar, and finally excessively elongated and attenuated, each bearing a single flagellum. The cells of the inner mass do not remain uniform in character but differentiate into the various cells composing the inner mass of the larva, such as spicule cells, contractile cells, cells of the future epidermis, and finally undifferentiated amœboid cells. With respect, however, to the exact composition of the inner cell mass of the larva, the statements of Maas and Delage are at variance. The larva is now fully developed and ready to leave the maternal body, which it does in all cases, probably, by the osculum.

The free swimming larva is oval in shape and covered with cilia, or rather flagella, over the whole surface in *Spongilla* and the horny sponges, but in the *Cornacuspongiæ* proper, i.e., the suborder *Halichondrina* of the *Monaxonida* of Ridley and Dendy, the flagella are absent at the hinder pole. Two distinct types can further be distinguished in the partially flagellated larvæ of *Cornacu-*

*spongiæ*, the one characteristic of the families *Desmacidonidæ* and *Axinellidæ*, the other of the families *Homorhaphidæ* and *Heterorhaphidæ* (Gellius). In the first type the layer of flagellated cells covering the anterior end and sides of the larva simply ceases towards the hinder end, and while the flagellated layer is coloured orange, red or scarlet, the inner mass protrudes posteriorly with no other colouring than that of ordinary protoplasm. In the second type the hinder end bears, in the region where the flagellated layer ceases, a circle of especially developed flagella of large size, which are stiffer than the other flagella, and more resemble bristles, and are carried upon a circle of correspondingly large cells. In addition to this peculiarity, the cells forming the surface at the hinder end of the larva are pigmented, the large flagellated cells being chiefly, though not exclusively, the seat of this pigment, so that the larva has at its hinder end a violet, brown, or yellow pigment ring, while the rest of the body is white. These differences of ciliation and pigmentation are such as to be easily recognised with a magnifying glass of low power or even with the naked eye. Larvæ of the first type have been seen in *Esperia*, *Myxilla*, *Desmacidon*, *Clathria*, *Dictyonella*, and *Axinella*, of the second type in *Reniera*, *Chalinula*, *Gellius*, *Pachychalina*, and *Toxochalina*. Maas thinks that the characters of these two types of larvæ are of systematic value, on account of the constancy with which they occur in various genera, and the fact that they coincide with other structural peculiarities both of the larva and the adult. A classification of the *Monaxonida* found on larval characters would place the families *Desmacidonidæ* and *Axinellidæ* of Ridley and Dendy in one group, and the families *Homorhaphidæ* and *Heterorhaphidæ* in another, in opposition to Vosmaer's classification, which brings together *Axinella* and *Homorhaphidæ*, on account of their lacking microscleres, while forms such as *Gellius* are placed with *Desmacidon* and *Myxilla*. It is interesting to note, however, that though *Gellius* possesses microscleres in the adult condition, its larva has macroscleres only and is more nearly related to forms without

microscleres, such as *Reniera*, than to the genera possessing chelæ (*Desmacidonidæ*).

From larva of the second type, with a ring of larger flagellated cells at the hinder end, there is an easy transition to the larvæ of horny sponges with their uniform covering of cilia. In the latter the ring of large cells has grown inwards to form a circular area, completely covering the hinder end. The larvæ of horny sponges, such as *Hircinia* and *Euspongia*, are thus more nearly allied to the larvæ of *Reniera* and *Chalinula* than to those of other *Monaxonida*, a relationship parallel to that shown by the structural characters of the adult sponges. In *Aplysilla*, however, the larva, as described by Delage, is without the pigment ring, and approaches more in other peculiarities also to the first type of larva; a fact which would point to a polyphyletic origin of horny sponges from different families of *Monaxonida*. In *Spongilla* also the uniform covering of cilia is to be explained by an overgrowth of the cells at the posterior pole, but its cells are different from those of horny sponges. The larva of *Aplysilla* differs, according to Yves Delage, from the other larvæ described by himself and by Maas, in that the inner mass is uncovered at the anterior pole.

The structure of the larvæ of siliceous sponges can only be determined by sections, on account of their opacity, and the statements of Maas and Delage differ somewhat with regard to this point. They are agreed upon the fundamental point that the larva is composed of two layers of cells—(1) an external layer of flagellated cells; (2) an inner mass containing spicules and several kinds of cells imbedded in a jelly-like substance. A cavity may persist at the anterior pole, probably a remnant of the segmentation cavity, or the larva may be compact. The two authors differ considerably, however, as to the exact composition of this inner mass and its relations to the outer layer. According to Delage the inner mass consists of a layer of epidermic cells placed immediately beneath the ciliated cells, and a central nucleus composed of amœboid cells and "cellules intermédiaires". According to Maas the

interior of the embryo is composed, at an early stage, of a uniform mass of granular macromeres, each with a vesicular nucleus. The first differentiation is that some of these become clearer and less granular, and commence to secrete spicules. These "scleroblasts" still retain, however, the vesicular nucleus. A part of the remaining blastomeres then becomes transformed into cells with uniform, finely granulated protoplasm and a nucleus containing a framework and evenly distributed chromatin; these cells are destined to give rise to epithelial, contractile and connective tissue cells. In addition there remain over a number of undifferentiated blastomeres, with coarsely granular protoplasm and vesicular nucleus. These are set apart to become the future amœboid and genital cells of the adult sponge, so that we have here an interesting and striking case of the germ cells being separated at an early period from the somatic cells and retaining the primitive characters of the blastomeres of the ovum. Hence the inner mass of the larva consists of (1) scleroblasts with spicules, the latter always having a definite arrangement, which in some species (*e.g.*, *Esperia Lorenzi*) may attain to a high degree of complication; (2) undifferentiated cells, corresponding to Delage's amœboid cells; and (3) differentiated cells, corresponding to Delage's "cellules épidermiques" and "intermédiaires"—a distinction which Maas does not recognise. Some of these differentiated cells, when bounding a free surface, as at the hinder end of the larva, take on an epithelial arrangement, but the cells so modified are not to be regarded as essentially different from those lying beneath them; their difference in appearance is due to the accident of their position, so to speak. Other differentiated cells again are often arranged radially or tangentially in the larva, and probably serve for the contraction of the body. In spite of the different elements it contains, Maas considers the inner mass as forming but a single germinal layer, and as a proof of this he points, on the one hand, to the destination of its cells in the adult sponge, and, on the other, to its origin from a uniform mass of macromeres in the embryo.

The larva is, therefore, to be considered as a *two-layered organism* from an embryological point of view.

The layer of flagellated cells consists, according to both authors, of excessively attenuated, columnar cells, each bearing a flagellum. The body of the cell is much thinner than the nucleus, so that for the sake of close packing the nuclei of this layer are obliged to lie at different levels, giving at first sight the appearance of several strata of cells, where in reality there is only a single layer. The nuclei are placed rather far from the outer surface, so that the entire layer of flagellated cells presents the appearance of an inner zone made up of closely-packed nuclei, four or more layers deep, and an outer clear, finely striated zone, the striations corresponding to the outlines of the attenuated cells. Only in *Spongilla* is the appearance somewhat different, since here the flagellated cells are not so attenuated, being of about the same thickness as their nuclei, so that the latter form a single stratum.

The accounts of Maas and Yves Delage differ also somewhat as regards the relation of the flagellated layer to the inner cell mass. According to the former author the flagellated cells form a more or less uniform layer covering the inner mass either completely or partially. The larva of *Axinella* is remarkable for the occurrence of peculiar gland-like cells placed at intervals between the flagellated cells, which strongly resemble in their characters the cells of the inner mass; *Esperia* also has peculiar cells, perhaps glandular, at the anterior end, external to the flagellated cells. According to Delage, on the other hand, the "cellules épidermiques" are entirely internal to the flagellated cells in *Spongilla*, and nowhere exposed on the surface; their situation is similar in *Aplysilla*, except that they are exposed at the anterior end, where the inner mass protrudes; but in *Esperia* and *Reniera*, on the contrary, they are mixed with the flagellated cells, "and might just as well be said to be external, were it not that they separate a little from one another to permit the necks, with the flagella, of the ciliated cells to pass out between them," while at the hinder end they are exposed and form part



of the surface. Maas, who does not recognise a distinction between the cellules épidermiques and the other differentiated elements of the inner mass, considers that what Delage has seen between the flagellated cells are glandular elements similar to those seen by him in *Axinella*.

The next stage in the life history is the fixation of the larva and its metamorphosis into a young sponge. The period of larval life is usually of short duration, and Maas lays it down as a general rule, that the longer fixation is delayed, the more likely is the subsequent development to become abnormal. Few organisms are so delicate or so liable to abnormalities as sponge larvæ, and it may be said that unless they are very carefully tended, anomaly becomes the rule. It is probably owing to this cause that the greatest confusion prevailed among earlier investigators as to the pole of fixation, though "the general statements are in favour of the attachment taking place by the posterior extremity where the granular matter projects" (Balfour, *Comp. Embryology*). On this point the statements of both our authors show a pleasing unanimity, to the effect that normally fixation always takes place by the anterior pole, *i.e.*, by the pole which in all but *Aplysilla* is ciliated.

With regard to the metamorphosis, the statements of Maas and Delage are again in agreement as to fundamental points, though differing greatly as to the details of the process. According to both authors, the cell layers composing the larva undergo displacements whereby the ciliated cells, which have temporarily lost their flagella, come to be placed in the interior and to be surrounded by the cells of what was formerly the inner mass. The whole organism becomes very much flattened and spread out after fixation, and is at first compact, but spaces soon appear in the parenchyma to form the canal system, round which the various cells group themselves. The ciliated cells give rise to the chambers alone, becoming the collar cells; the flattened epithelium lining the canals and covering the outer surface, as well as the entire mesoderm, are derived from the inner mass of the larva.

According to the account given by Maas, the process by which the two layers of the larva shift their position is mainly as follows. The larva fixes by the anterior ciliated pole and the granular cells at the hinder pole burst out, if they were not already exposed in the larva, and grow round the mass of ciliated cells by a kind of epibole. Especially instructive for the understanding of this process is a figure given by Maas [(2) pl. xx., fig. 19], representing a section of a larva of *Clathria coralloides* preserved a few minutes after fixation, showing the inner mass flowing out, as it were, from the hinder pole and round the flagellated cells. As a result the cells of the inner mass come to completely surround the flagellated cells, which have lost their flagella and form a compact mass of cells in the interior; just as do the collar cells in greatly contracted tubes of *Ascetta clathrus*.<sup>1</sup> Thus the two layers of the larva, easily distinguished by the smaller and more brightly staining nuclei of the former flagellated cells, have become exactly reversed in position. A period of apparent rest now takes place, the larva having become greatly flattened, with an actively amœboid margin. During this period an interpenetration of the two layers is taking place rapidly. At the end of this period the larva commences to increase slightly in size, owing to the formation of cavities in the interior. Lacunæ arise of two kinds: the one, the future exhalant canals, appear in the mass of cells with small nuclei, the former flagellated cells; the other, the future inhalant canals, arise in the outer parenchyma, derived from the inner mass of the larva. The flagellated cells arrange themselves in little groups along the efferent lacunæ, each group becoming a chamber, the cells regaining their flagella and forming collars. The epithelium lining the efferent canals arises, however, from cells of the inner mass of the larva, and is not, as hitherto sup-

<sup>1</sup> See the figures given by v. Lendenfeld (*Zeitschr. f. wiss. Zool.*, bd. liii., pl. ix., fig. 30) and myself (*Quart. Journ. Micr. Sci.*, N.S., vol. xxxiii., pl. xxix., fig. 14).

posed, of "endodermal" origin.<sup>1</sup> The flagellated epithelium of the larva is entirely used up in forming chambers. The differentiated cells of the inner mass of the larva form (1) all the flattened epithelium of the adult sponge, (2) its contractile cells and sphincters, (3) the connective tissue elements and spongoblasts. There remain only the scleroblasts and the amœboid and sexual cells, the origin of which from the inner mass we have already traced.

The canal system thus formed soon acquires a communication with the exterior by pores and an osculum, and the organism becomes a young sponge. It is interesting that both our authors are agreed in regarding the pores as *intracellular* ducts, as described by Bidder and myself in Ascons.

The account given by Yves Delage of the metamorphosis differs from that of Maas, as has been said, with regard to the details of the process, and he describes a series of events which are without a parallel in the animal kingdom, and which are certainly a tax upon our credulity. We have seen that he describes the larva as consisting of an outer layer of "cellules ciliées," with beneath this a layer of "cellules épidermiques," and an internal nucleus of "cellules intermédiaires" and "amœboïdes," the last-named elements being marked out by their large size, coarsely granular contents, and vesicular nuclei. At the metamorphosis, according to him, the épidermiques come to the surface and form a layer covering the ciliées, this change of position not being effected by any process of epibole or overgrowth, but by each epidermic cell struggling up to the surface independently and passing between the ciliated cells over it, which separate to permit of its migration.

At the same time a most extraordinary process is going on. The large amœboid cells of the interior send

<sup>1</sup> In his first paper (1) Maas regarded the epithelium lining the exhalant canals as derived, together with the chambers, from the ciliated layer of the larva, a view which in his later paper (2) he abandons.

out pseudopodia towards the surface, which touch the ciliated cells. The latter have in the meanwhile drawn in their flagella and become rounded. When the process of an amœboid cell reaches a ciliated cell it immediately seizes it and devours it, after the manner of a phagocyte. In this way all the ciliées in *Spongilla*, and the greater number of them in *Esperia* and *Reniera*, become captured by the amœboid cells and carried into the interior of the sponge. When full fed, so to speak, the amœboid cells retract their pseudopodia and become rounded, forming a number of "groupes polynuclées" in the interior of the larva. Each such group consists of a central vesicular nucleus, that of the amœboid cell, and round this a number of brightly staining small nuclei, derived from the ciliated cells. The latter, after being thus engulfed, alter in appearance. Their protoplasm forms a clear zone round the nucleus, but is often indistinguishable. The nucleus contracts become opaque and uniform, stains strongly with carmine, and has the appearance of a simple granule. In fact these are the granulations which have been mistaken by Maas and Götte for yolk granulations.

We now have the larva composed of cellules épidermiques externally enclosing a parenchyma of intermédiaires and groupes polynucléaires, each of the latter being an amœboid cell which has devoured a number of ciliées. After a short time further changes go on in the amœboid cells. Their captured nuclei begin to swell and to separate one from another. The amœboid cell as a whole begins to enlarge itself and become irregular in form, sending out lobes which fuse with the similar lobes of adjacent cells to form a vast syncytial network, in the meshes of which are the cellules intermédiaires of the larva. Where there are a certain number of ciliées not captured by the amœboid cells, they also take a part in this syncytium. Some of the meshes of the syncytial network close up, others expand to form lacunæ, the future canal system. The captured nuclei of the ciliées travel to the surface of the amœboid cells, regain their former appearance, and begin to arrange

themselves in hemispherical groups, which become the future chambers. The cellules intermédiaires, which we last saw in the meshes of the syncytial network, begin to flatten and arrange themselves round the exhalant lacunæ to form their epithelium. Those of the intermédiaires not used up in this way become the connective tissue of the adult. The amœboid cells, after disgorging their prey, become the wandering cells of the adult. Occasionally, however, some of the ciliated cells become actually digested when engulfed by the amœboid cells.

The above assertions of Delage with regard to the process of metamorphosis are certainly such as zoologists will find it difficult to credit without very strong proofs of their correctness. The following reasons are advanced by him in support of his statements: in *Spongilla*, where this process of cannibalistic phagocytosis is most complete, there are to be found in the interior of the sponge, at the commencement of the second day, neither chambers nor free cells in sufficient number to give rise to them. Apart from the spicules there is nothing beneath the epidermis except the groupes polynuclées and the cellules intermédiaires. At this period small cells begin to appear, at first few, but soon innumerable, which arrange themselves to form the chambers, and in proportion as these cells appear the granules in the groupes polynuclées disappear. When the chambers are fully formed the groupes polynuclées have disappeared, leaving in their place only the amœboid cells. "There is thus an evident correlation between the newly appeared cells and the globules of the groupes polynuclées." If these globules were vitelline granules they should gradually diminish and disappear, but, on the contrary, at the moment when the new cells appear the globules increase in size and separate from the amœboid cells.

Moreover, if the countless cells which form the chambers do not come from these globules, they should be derived from pre-existent elements, either from the amœboid cells or the intermédiaires, which one would expect to find in active division. But, as a matter of fact, neither the one

nor the other divide at all actively, mitoses or dividing nuclei being of exceptional occurrence. Finally, Delage admits, and shows plainly in his figures, that the globules of the groupes polynuclées are very different from the nuclei of the free ciliées before and after being devoured; and, further, that when, as in *Esperia*, all the ciliées are not devoured, their nuclei retain their normal character in the syncytium, while they appear strongly modified in the amœboid cells. He declares, however, that he has found every transition between the opaque, strongly stained globules, and the much larger, oval nuclei of the ciliées, with their membrane and granular contents. He also figures pseudopodial processes of the amœboid cells reaching to, and apparently capturing, cells of the ciliated layer.

In opposition to the arguments of Delage, Maas urges that Delage's methods are not adequate to determine the existence of such a process of phagocytosis, since he has never observed it directly, but only inferred its occurrence from a comparison of sections. In objects of such excessive minuteness as the cells of the larvæ of siliceous sponges it is often impossible to make out clearly whether the nuclei of the ciliées be *in* or *on* the amœboid cells. Moreover, Maas was able to repeat in *Esperia* the observation he formerly made in *Spongilla*, namely, that after double staining with borax carmine and malachite green, the latter stain colours the granules in the amœboid cells, but not the nuclei of the flagellated cells. Delage does not seem to have succeeded with this reaction. Finally, Maas draws attention to the difference in the degree to which this process is described as occurring in different species, and the fact that, according to Delage himself, a number of free flagellated cells are to be met with in all stages of the metamorphosis. Maas is willing to admit that flagellated cells may occasionally be devoured by amœboid cells, but regards this as pathological.

A decision on this question can, of course, only be obtained by investigation of the objects. On the whole, however, Delage's statements with regard to the phagocytosis and the formation of the syncytium do not seem

to be beyond all doubt. We miss in all his figures any indication of cell outlines, and he does not seem to have made use of methods calculated to show them up. Had he done so it is possible that his groupes polynuclées might have turned out to be only ciliées closely packed round granular amœboid cells, which is indeed the impression some of his figures give. The syncytium formed by the undevooured ciliées seems equally doubtful. Sections of greatly contracted tubes of *Ascetta clathrus* prepared by ordinary methods show a similar closely packed mass of cells, without apparent cell outlines, in the interior. There is no reason to suppose, however, that cell boundaries are really wanting, for each cell is derived from a single collar cell, and becomes such again when the sponge expands to its normal condition. Moreover, by suitable methods of maceration the cells in this apparent syncytium can be isolated from one another.

The researches of Maas and Delage, complete as they are, leave many interesting questions to be decided by future investigators, questions upon which it is impossible to pronounce more than an opinion meantime. If the present writer, after having been an eye-witness of Dr. Maas's investigations, and having had the opportunity of studying his preparations, is more inclined on that account, as well as on general grounds, to take Dr. Maas's view of the questions at issue, it is from no wish to detract from the value of the beautiful investigations of M. Yves Delage. And, as we have seen, our authors are entirely agreed upon more fundamental points, so that, to briefly recapitulate, we may draw up the following typical course of development for a siliceous sponge.

The segmentation is unequal, leading to the formation of micromeres at one pole and macromeres, containing the yolk, at the other. Later on the micromeres are found more or less completely surrounding the macromeres. The micromeres become a ciliated epithelium, and the larva is hatched consisting of two layers: (1) an external layer of flagellated cells, (2) an inner mass of various kinds of granular cells, which are either completely internal, or protrude posteriorly,



rarely anteriorly as in *Aplysilla*. The larva fixes by the anterior pole, and the granular cells come to surround the flagellated cells. The latter give rise to the collar cells of the adult, while the granular cells form (1) all the flattened epithelium, and (2) all the mesoderm, so called, of the adult sponge.

The resemblance of this type of development to that occurring in *Sycon*, with its amphiblastula larva, is obvious. The flagellated cells of the amphiblastula correspond in origin, position, and destination to those of siliceous larvæ. The granular cells, in like manner, of the amphiblastula, are homologous with the inner mass of the siliceous larvæ. Delage admits that the cellules intermédiaires and amœboïdes of his larvæ, while wanting in the amphiblastula of *Sycon*, "are yet potentially contained in the granular cells," which he regards as equivalent to the épidermiques. "The larva," he says, "of *Sycandra* can be considered as a larva of *Esperia* or *Reniera* reduced to the cells of its external envelope," with the epidermic cells confined to the naked pole. This homology between the granular cells of *Sycon* larvæ, and the whole inner mass of the siliceous sponge larva, is, as Maas points out, an additional argument for regarding the latter as representing a single layer. In the amphiblastula, the flagellated layer is less strongly developed, and does not enclose the granular cell mass. Not only, however, do variations in this respect occur in siliceous larvæ, but the existence of a so-called pseudogastrula stage has long been known in Sycons, in which, shortly before the larva leaves the maternal tissues, the granular cells are almost entirely surrounded by the flagellated cells. The segmentation of the ovum, the embryonic development of the larva, and the metamorphosis are all very similar in the two larvæ. Delage points out that the invagination of *Sycon*, the so-called amphigastrula, and the penetration of the flagellated cells into the interior in siliceous larvæ are "two phenomena . . . of fundamentally the same order," but this is even more the case if we accept Maas's account of the metamorphosis.

While there is thus a close agreement, extending even to details, between the life-histories of the great majority of both calcareous and siliceous sponges, the development of the most primitive forms in the two groups presents great difficulties. This is especially the case in the Ascons, where, on account of the primitive nature of the adult forms, we might expect to find an equally primitive mode of development, which would furnish the key to that occurring in other sponges. But if the description hitherto given of the development of *Ascetta* be correct, any comparison with the larva of *Sycon* or of *Cornacuspongiæ* is out of the question.

According to the accounts of Schmidt<sup>1</sup> and Metschnikoff,<sup>2</sup> the larva of *Ascetta* is hatched as an oval blastula composed of a single row of flagellated cells enclosing a large cavity. The cells at the hinder end differ in some characters from the remainder, being in particular more granular. From the hinder pole an immigration of cells goes on into the interior, until the internal cavity becomes packed with large, granular cells, with nuclei considerably larger than the nuclei of the ciliated epithelium covering them. The larva thus constituted fixes, by which pole is not certain, and the covering of flagellated cells is said to furnish the flattened ectoderm of the adult, while the cells of the internal mass form the collar-cell layer.

If the destination of the two cell layers of the larva of *Ascetta* be really as described, there is no possibility of comparing it with the amphiblastula, or with the larvæ of *Cornacuspongiæ*. In the face, however, of the close resemblance of the larva of *Ascetta* just before fixation and the completely ciliated larvæ of some *Cornacuspongiæ*, it is difficult to escape the conviction that the metamorphosis of *Ascetta* has been quite wrongly described. In both larvæ we have a layer of finely granular flagellated cells sur-

<sup>1</sup> Schmidt, Das Larvenstadium von *Ascetta primordialis* and *A. clathrus*, *Archiv f. mikr. Anat.*, bd. xiv., 1877.

<sup>2</sup> Metschnikoff, Spongiologische Studien, *Zeitschr. f. wiss. Zool.*, bd. xxxii., 1879.

rounding an inner mass of coarsely granular cells with large nuclei. It seems almost impossible to believe that the flagellated cells in the larva of *Ascetta* do not, as in the other type, become converted into the collar cells of the adult. Such a reversed development would involve grave morphological difficulties, and there are in addition histological reasons against its occurring. In the adult *Ascetta*, as in other sponges, the nuclei of the collar cells are the smallest in the sponge, their diameter being in fact scarcely half that of the ectoderm cells. In the flagellated cells both of the *Ascetta* larva<sup>1</sup> and of the larva of *Cornacuspongiae* the nuclei are similarly very much smaller than those of the inner mass.

What in all probability really takes place in the development of *Ascetta* is that the larva fixes by the anterior pole, the inner mass bursts out at the posterior (upper) surface, and grows round the flagellated cells, which thus come to lie internally, just as they do in *Sycon* or *Esperia*.<sup>2</sup> This supposition becomes still more probable if Metschnikoff's figures be carefully studied in the light of this theory, especially figs. 13, 14, 15 of his tafel xxiii.<sup>3</sup> These three figures can easily be interpreted, as Maas has pointed out, as representing the bursting out of the inner mass (fig. 14) and its growth round the flagellated cells (fig. 15).

<sup>1</sup> Compare especially the figures of Schmidt, *loc. cit.*, taf. xv.; figs. 5, 6 and 7.

<sup>2</sup> The above conclusions were arrived at by me, as Maas has kindly stated [(2), p. 419, footnote], when I was giving a course of lectures on sponges at Oxford in 1892. At that time only Maas's work on *Esperia* (1) and the two preliminary accounts of Delage had appeared (*Comptes Rendus*, cx., p. 654, and cxiii., pp. 267-269). I wrote to Dr. Maas and asked him his opinion on the subject, and in his answer to my letter he expressed the same opinion as I had already arrived at, and which he has since published. Just after this Delage's work (1) appeared, stating the same opinion again. M. Delage of course has the priority in the matter, but it is interesting that three naturalists in three different countries should have simultaneously and independently formed the same views upon this subject. It will be still more interesting when some investigator describes how *Ascetta* really does develop.

<sup>3</sup> *Loc. cit.*

Metschnikoff interpreted these appearances as a gradual flattening of the flagellated cells to form the outer cell layer of the adult. A precisely analogous misinterpretation of such appearances was made by Maas himself, who, in his former work<sup>1</sup> on the development of *Spongilla*, described the ciliated cells as flattening to form the ectoderm of the adult, though he now recognises that the appearances seen were due to the cells of the inner mass growing over the flagellated cells. Moreover, O. Schmidt, in deriving the adult ectoderm of *Ascetta* from the flagellated epithelium of the larva, was obliged to assume a fusion of several flagellated cells into the large amœboid cells of the young sponge, which is, to say the least, improbable.

For all these reasons we are justified in saying that the derivation of the ectoderm of *Ascetta* from the flagellated cells of its larva is neither proved, as a matter of fact, nor probable in theory, since only on the contrary supposition would it be possible to compare the larva of *Ascetta* with the larva of *Sycon* and siliceous sponges. A study of the literature of sponge embryology shows that nearly all investigators have been dominated by the idea that ciliated cells in the larva must become ectoderm in the adult, perhaps from a false analogy with Cœlenterate development. This superstition, as one might call it, was first overthrown by Metschnikoff and Schulze in *Sycon* twenty years ago; it still remained, however, to confuse sponge embryology, until Delage and Maas showed its falsity in the case of siliceous sponges. It now remains for some fortunate investigator to establish the origin of collar cells from flagellated cells in the larva in the few cases where assertions to the contrary still hold the field.

After what has been said with reference to *Ascetta* it is hardly necessary to discuss the developments of *Hali-sarca* and *Plakina*, where the appearances seen seem to have been similarly misinterpreted. The development of *Oscarella*, however, requires a brief discussion. Here the larva is hatched as an oval blastula composed of a single

<sup>1</sup> *Op. cit.*

layer of columnar flagellated cells, those at the posterior end being broader, more granular, and with larger nuclei than those anteriorly. After a short time one pole of the larva is invaginated into the other, but in this process abnormalities are frequent, and it is not certain which method is normal; Heider<sup>1</sup> believes that normally the posterior pole is invaginated into the anterior. The larva fixes by the orifice of invagination, and the invaginated cells become the collar cells.

Delage's explanation of this development is that the cells of the blastula constitute an indifferent layer, containing potentially both endoderm and ectoderm, which only become differentiated after fixation.

Maas, on the other hand, regards the blastula, so called, of *Oscarella* as really equivalent to the amphiblastula of *Sycon*, the hinder granular cells of the former being the equivalent of the granular cells of the latter, with the difference that the granular cells of *Oscarella* are ciliated, as in the adult ectoderm. He thinks that normally the anterior pole of the larva is invaginated into the posterior, a process strictly comparable to the invagination of the *Sycon* larva or the overgrowth of the flagellated cells in siliceous sponge larvæ.<sup>2</sup>

Maas's view seems the most probable, for an additional reason which both he and Delage have overlooked. In 1884 Sollas<sup>3</sup> published a memoir on the development of *Oscarella*, in which he arrived at the conclusion that the embryo developed into a young sponge before leaving the maternal tissues, a conclusion which was justly set aside and refuted by Heider. What Sollas really did show, however, was that the embryo undergoes a *distinct invagination* before leaving the mother sponge, an invagination

<sup>1</sup> Zur Metamorphose der *Oscarella lobularis*. *Arbeiten d. Zool. Inst. Wien*, bd. vi., 1886.

<sup>2</sup> I expressed exactly the same opinion as that put forth here in my lectures in 1892, without, however, having discussed the matter at all with Dr. Maas.

<sup>3</sup> *Quart. Journ. Micr. Science*, N.S., xxiv., 603-621, pl. xxxvii.

which we may compare directly with the so-called pseudo-gastrula of *Sycon*. If this comparison be valid, then the free-swimming larva is not to be regarded as a blastula; this stage is passed over in the maternal tissues, and is to be seen in figs. 20a and 18 of Sollas's plate xxxvii. The blastula proper is followed by an invagination, as we see clearly in figs. 33, 34, 19, 27, etc., in spite of the distortion that Sollas's specimens seem to have undergone. We must next suppose that at the time of leaving the mother the embryo again assumes a blastula form, *just as is known to occur in Sycon*. Then the free-swimming larva would exactly represent a modified amphiblastula. Whether these assumptions are justified or not, it is at least clear from Sollas's figures that an invagination does go on in the maternal tissues.

We have now discussed the chief types of sponge development, and starting from the well-ascertained facts of the development most usual both in calcareous and siliceous sponges, certain assumptions have been made with regard to the course of development in the more primitive forms, such as the *Ascons*, *Halissarca*, *Oscarella*, and *Plakina*. How far can we now construct a type or fundamental plan of development for sponges in general?

Taking into consideration all the modes of development as yet known, the following is perhaps the most primitive type. The egg by segmentation gives rise to a hollow blastula composed of a single row of flagellated cells, which, perhaps, were originally all alike, but in all forms known to us differ to some extent at the two poles, usually markedly so. The cells of the hinder pole become displaced into the interior, by immigration (*Ascetta*), invagination (*Oscarella*) or epibole (*Sycon* and siliceous sponges generally). We now have a two-layered larva, and so far the development does not differ in any essential point from what we know in other Metazoa, but events which now come about are altogether peculiar to sponges. The inner mass bursts out and envelops the flagellated layer which was before external to it. This is the so-called amphiblastula, followed by the amphigastrula stage. The

ciliated cells now develop into the collar cells of the adult, reverting probably to their primitive condition in the blastula. The inner mass of the larva becomes the outer layer (ectomesoderm) of the sponge. *Ascetta* is hatched in the true blastula stage, and on this account, and also from the fact that its inner mass arises by immigration, is perhaps more primitive in its mode of development than any other form. *Spongilla* and the horny sponges appear to be set free when the inner mass is still quite internal; from this condition we find transitions through the *Halichondrina* to a complete amphiblastula larva as in *Sycon* and *Oscarella*. No sponge is hatched at a stage later than this.<sup>1</sup>

If we wish to compare the development of sponges with that of other animals, and to discuss their relation to the germ-layer theory and their position in the animal kingdom, two courses are open to us. We may either (1) start from a comparison of an adult sponge, such as *Ascetta*, with an adult Coelenterate, such as *Hydra*, in which case we should term the ciliated layer *endoderm*, the outer layer *ectoderm*; or we may (2) compare the typical life-histories of a sponge and a Coelenterate, and then we should term the ciliated layer of the sponge larva *ectoderm*, its inner mass *endoderm*. The former view was Schulze's, the latter Balfour's.

Maas is of opinion that, if the germ layers of sponges and other Metazoa are to be compared at all, the ciliated cells of the larva are ectoderm, the inner mass endoderm. Only in this way is an explanation possible for the unequal segmentation and the invagination of the macromeres into the micromeres, *i.e.*, the wrongly termed pseudogastrulation. If the opposite view be taken, not only does the pseudogastrula remain inexplicable, but the displacement of the ciliated cells into the former inner

<sup>1</sup> *Cliona*, the boring sponge, extrudes its ova, which develop outside the sponge, but in other respects the development appears to be similar to that of *Cornacuspongia*. The larva is completely ciliated. See Nassonow, *Zeitschr. f. wiss. Zool.*, bd. xxxix., 1883, pp. 298, 299.



mass must be regarded as the true gastrulation. A process can, however, hardly be termed gastrulation when the preceding stage is a solid larva, as in siliceous sponges, and when the future "ectoderm" is entirely internal. An ectoderm containing the yolk and lying internally to the endoderm is a paradox.

Maas considers the sponges true Metazoa on account of their reproduction by ova and spermatozoa and the differentiation of their tissues. They are derived from two-layered ancestors, of which the two layers are comparable to the ectoderm and endoderm of other Metazoa. The difficult thing to explain, from a phylogenetic point of view, is the complete reversal in position which their layers have undergone. This must have been in some way the result of a change in their mode of nutrition, whereby the flagellated ectodermal cells retained their structure, but changed their place and became carried into the interior to become the collar cells of the sponge. Sponges are in no case to be ranked with Cœlenterates, since their inner and outer layers are not homologous with the corresponding layers of Cœlenterates, and their canal system is of absolutely different origin.

Delage, on the other hand, regards the sponges as descended from a colony of Protozoa, represented by the blastula in ontogeny. They are descended from the Protozoa entirely independently of other Metazoa, and their layers are not to be compared with the germ layers of Metazoa. They show a progressive differentiation of their tissues, which, however, does not take place in the sense of a germ-layer formation as in higher animals, but by means of division of labour among the cells of the colony, so that some become epithelial, others skeletal, and so forth.

These, however, are questions upon which at present, at any rate, no final decision is possible, nor need one be attempted here.

RECENT LITERATURE.

- (1) DELAGE, YVES. Embryogénie des Éponges. Développement Post-larvaire des Éponges Siliceuses et Fibreuses Marines et de l'eau douce.  
*Archives de Zoologie Expérimentale et Générale* (2), x. (1892), pp. 345-498, pls. xiv.-xxi.
- (2) DELAGE, YVES. Note additionnelle sur l'Embryogénie des Éponges.  
*Ib.* (3), i., Notes et Revue, pp. iii.-vi. (Contains remarks on MAAS (1), and claims priority for certain statements.)
- (1) MAAS, O. Die Metamorphose von *Esperia Lorenzi*, O.S., nebst Beobachtungen an anderen Schwammlarven.  
*Mittheilungen aus der Zoologischen Station zu Neapel*, bd. x., heft 3, pp. 408-440, taf. xxvii., xxviii.
- (2) MAAS, O. Die Embryonal-Entwicklung und Metamorphose der Cornacuspongien.  
*Zoologische Jahrbucher Abtheilung für Anatomie und Ontogenie der Thiere*, bd. vii., pp. 331-448, taf. xix.-xxiii.

E. A. MINCHIN.

## SOME ASPECTS OF THE IMMUNITY QUESTION.

IT is well known that the refractory state of an organism to diseases produced by bacteria or by toxins may be either absolute or relative, further, the conception of immunity may include the whole organism or certain of its constituent tissues and organs, and finally, the immune condition may be natural or acquired. It is in connection with acquired immunity that such an enormous literature has accumulated since 1887. Previous to this date the methods employed to confer immunity consisted either in the inoculation of specific virus, in the preventive inoculation of specific micro-organisms which were artificially attenuated by the action of heat, compressed air or carbolic acid, as was practised by Pasteur, Toussaint, Chauveau, Arloing, Cornevin and Thomas, or in the inoculation of absolutely inoffensive bacteria which had lost their pathogenic property, a method employed by Chauveau for anthrax and Hüppe for chicken cholera.

The preventive injection of sterile filtered cultures of pathogenic bacteria marked an important advance in methods for producing immunity; and this was definitely demonstrated about seven years ago by the researches of Salmon and Smith (1) on hog cholera. In this country Wooldridge (2) succeeded in protecting rabbits against anthrax by the injection of filtered cultures obtained from a growth of bacillus anthracis on a proteid (a nucleo-albumin) prepared from the testis and thymus gland, a substance which has no protective action before multiplication of the bacilli. His experiments have been verified (3), and around this fertile discovery considerable discussion has arisen. In the succeeding year, the bactericidal action of blood or serum was discovered by Nuttall (4) and confirmed by many observers. The advance in the study of immunity made by Wooldridge may be gathered from his own words; as his discovery was made at a time "when the few cases in which protection

against zymotic disease had been found to be possible, this had been effected by the communication to an animal of a modified form of the disease against which protection was sought".

Since natural and acquired immunity are possibly different in principle and even dependent upon various causes, many conceptions have arisen as to the origin of this condition, which subsequent investigation has not verified so as to remove the ideas from the position of hypotheses. The immune condition has been considered to be related to the exhaustion or lack of suitable material on which the micro-organisms of infective disease could thrive. General or local modifications in the metabolic activity of the cells of the organism have also been held to be the cause of immunity. This has found its maximum development in the idea of phagocytism, where not only leucocytes (Metschnikoff, 1883) but the cells of the fixed elements of connective tissues play an important *rôle* by the inception and subsequent destruction by chemical means of specific pathogenic germs. Criticism of the phagocyte theory in Germany led to the discovery of the bactericidal action of blood and serum, while the possession of antitoxic properties by the body fluids of animals rendered artificially immune against tetanus or diphtheria, supported the theory that definite antibacterial, or antitoxic substances, are present in the immune organism. The work of Buchner (5) and Hankin (6) falls in this period, and the latter was successful in isolating a bacteria-killing globulin. In his own words: "Immunity, whether natural or acquired, is due to the presence of substances, which are formed by the metabolism of the animals rather than by that of the microbe, and these possess the power of destroying either the microbe against which immunity is possessed, or the products on which their pathogenic action depends" (7). Buchner has re-defined his attitude on this question quite recently, and, while criticising the work of Behring, the real founder of the hypothesis that immunity was due to the antitoxic property of blood towards the toxins of tetanus and diphtheria, maintains that neither *in vitro* nor within the

body is the toxine of tetanus destroyed by the anti-toxine of the blood or serum. These bodies re-act only by the mediation of the organisation of the body. The term antitoxine is a misnomer, since it is a substance which only under certain circumstances confers immunity, and this it can only effect when actively operative within the organism (8). It is not necessary here to discuss either this view or the one that is opposed to it, which, while not denying that there may be methods of protection other than phagocytosis, affirms that the part played by phagocytic action is of all these the most widely spread and the most efficacious. The part played by eosinophile cells in the acute leucocytosis, which occurs at the seat of inoculation of micro-organisms, has been pointed out by researches in this country. When we consider the conflicting views as to the origin of the immune condition, the various grades of this, the distinction between the really immune condition where a pathogenic organism cannot multiply within the body, and the toxine-resistant state where the animal experimented upon is not invaded by micro-organisms and is at the same time refractory to the toxins these produce (9); the distinction between passive and active immunity, drawn by Ehrlich; the temporary duration of artificial immunity, and the impossibility of employing any test other than a physiological one for determining the variability of the refractory state, it becomes abundantly evident from the complexity of the subject that no absolute statement as to the origin of immunity is possible, and, further, statements relative to the behaviour of any specific pathogenic microbe within the body can only be employed with limitations when considering the mode of action of any other micro-organism.

A measure of experimental immunity or degree of toxine-resistance can be mathematically obtained by Ehrlich's method (10), where any grade of resistance is expressed by a number which gives the multiple of the lethal dose for normal individuals of equal weight, which the tested animal can withstand without death. The method of Behring and Wernicke (11) also indicates the degree of immunity by a

number which shows how many grammes of experimental animal one gramme of protective serum will protect against a certain lethal dose twenty-four hours after the introduction of serum, since injection of this does not immediately yield its full protective value (12).

Natural immunity undoubtedly is not dependent upon any single cause. It is well known that living vegetable tissues, such as the fruits and tubers of certain plants, most of which have an acid reaction, are free from bacterial growth. Warm-blooded animals are normally refractory to saprophytic and putrefactive micro-organisms, which flourish readily on dead tissues, and a natural immunity to the infective pathogenic bacteria of warm-blooded animals is enjoyed by most poikilothermous animals. This natural immunity can, however, be broken down. Frogs and lizards are refractory to anthrax, but as was shown by Gibier (13) and Metschnikoff (14) become susceptible when maintained at a temperature above  $25^{\circ}\text{C}.$ , and it has been recently observed that a frog when warmed to  $25^{\circ}\text{C}.$  loses its immunity if suddenly changed from a medium of  $15^{\circ}$  to one of  $25^{\circ}$ , though on gradual transition from  $12^{\circ}$  to  $25^{\circ}$  the immune condition is preserved (15). Under certain circumstances animals naturally immune against definite micro-organisms become invaded by these when the blood corpuscles are destroyed in quantity by such drugs as pyrogalllic acid or acetyl-phenyl-hydrazin, and under these conditions pathogenic germs which locally affect the organism are capable of spreading throughout the whole body (16). The introduction of the blood serum of one animal into the veins of another, the dog into the rabbit, would also produce the same effect. The researches of Leo (17) are well known. He attempted to break down the immunity which white mice present to the infection of glanders by treating these with doses of phloridzin, a drug which produces physiological diabetes. This disease, like carcinoma and chlorosis, is accompanied with wasting, though the subjects of the latter diseases are by no means so liable to the invasion of micro-organisms as are diabetics. Groups of animals were treated with phloridzin

alone, with inoculations of either *bacillus anthracis*, *bacillus tuberculosis*, or *bacillus mallei*, and thirdly with doses of phloridzin and inoculations of these bacilli. The experiments with anthrax and tubercle were negative; but of white mice treated with phloridzin by the mouth and intraperitoneal injections of *bacillus mallei* forty-seven out of forty-nine individuals died within three to nine days, and among forty-eight mice treated with phloridzin alone, none succumbed. The conclusions drawn from these experiments are that the blood of white mice contains a bactericidal substance and this power is injured by the presence of sugar or of phloridzin in the blood. Charrin and Roger (18), working on the well-known immunity presented by rats to anthrax, have also shown that fatigue is capable of inducing susceptibility. Like fatigue, currents of cold air will profoundly affect the metabolism of the body (19), and in the case of rabbits and guinea-pigs these agents increased the natural susceptibility to anthrax. Feeding these animals on liquid food also augmented their susceptibility (20). The normal resistance of rats to anthrax is stated by Feser to be considerably weakened when these animals are fed on a vegetarian diet, and Hankin (21) has confirmed these results, using groups of animals which fed on meat and bread, and on bread alone; in the latter case the susceptibility was induced and the spleens of these animals contained only traces of defensive proteid, while the spleens of the first group yielded abundance of this substance.

The necessity of the vital concurrence of micro-organisms for the production of infective diseases has long been a theoretical conception, and with regard to the infection by *bacillus maligni œdematis* and *bacillus tetani* this appears to be verified. It has been shown that the pathogenic properties of the former are not marked, owing to non-development, unless some of the culture material is also introduced, or if there is an admixture of the *proteus vulgaris* or *micrococcus prodigiosus*. Under these circumstances both the non-pathogenic and pathogenic microbes develop, and an active infection with characteristic symptoms of œdema and gas formation at the place of injection occurs. Further,



although an exquisitely anaërobic germ, the bacillus maligni œdematis grows excellently and maintains its virulence upon agar or gelatine when the above-named micro-organisms are associated with it (22). These results confirm in every respect the earlier observations of Roger (23). That rodents possess an immunity against the inoculation of young cultures of tetanus bacilli or the spores has been established by Vaillard and Vincent (24), who have shown that neither the bacilli nor the spores develop when these alone are introduced into the system. By using young toxine-free bacilli, or by employing spores absolutely freed from toxine, either by warming at  $65^{\circ}$  for twenty minutes, or by repeated washing with water, it was found that, owing to non-development within the organism, the effect of injecting even 1 c.cm. of spore culture was inoperative, in other words the tissues were exceedingly resistant to the microbes, or, at any rate, offered an unfavourable soil. This inoculation could, however, be rendered successful if a trace of lactic acid or trimethylamin, or a non-pathogenic micro-organism, such as bacillus prodigiosus, was simultaneously injected. The natural tetanus inoculation accordingly cannot occur without the association of other bacteria; these play the part of the toxine, which is generally introduced with the pathogenic bacilli, and this is decisive as to the results of injection. This multiplication easily occurs in a suppurative wound, where a local destruction of tissue is taking place. This symbiotic life of the tetanus bacilli is, however, not supported by other observers (25), but a renewed study of this question enables Vaillard (26) to maintain his former position. Among the recent literature dealing with Pfeiffer's influenza bacillus it has been pointed out by Weichselbaum (27) that the organism attacked by influenza becomes exceedingly favourable for the development of the diplococcus pneumoniae, and even in typical uncomplicated cases this latter micro-organism is frequently observed.

Defensive proteids or alexines have been isolated from the spleen and lymphatic glands by Hankin, and from the blood serum by Ogata, Tizzoni and Cattani, and it has been believed that the immune condition may be related to the

function of some of these organs. After extirpation of the spleen the latter observers (28) have found that rabbits cannot be rendered refractory to tetanus by the introduction of the serum of an immune animal. The part played by the spleen might therefore be due to the fact that this organ either produced a protective substance from the injected serum, or rendered the toxic bacterial products innocuous. A continuation of this research (29) however seems to show that the spleen plays no direct part in the production of immunity, and that if there is a specific protective substance it is not existent in this organ. Experiments have also shown that removal of this organ either before or after protective inoculation has no influence whatever on the acquired immunity of rabbits against the bacillus pyocyaneus (30). The most recent work bearing upon this question is that of Benario (31). This observer removed the spleens of rabbits and mice and then succeeded in rendering these animals immune to tetanus or to a lethal dose of ricin or to infective bacilli. Since extirpation of this organ has no influence whatever on the production of acquired immunity against an intoxication, a vegetable toxalbumin or an acute infective disease, the view that the refractory state is connected with the function of this gland can no longer be sustained.

The thyroid, thymus and lymph glands have also been regarded as an apparatus (33) where the various intermediate products which are assumed to be formed by the normal destruction of proteids within the circulation are rendered harmless. This view corresponds to some extent with the antitoxic function, which was at one time ascribed to the liver by Schiff. To test the part played by these organs experiments have been made upon extract of thymus gland (33), an organ which may be regarded as a mass of phagocytes. The bacilli of tetanus, cholera, diphtheria, typhus, erysipelas, anthrax and hog-erysipelas were grown either upon sterile aqueous thymus extract or upon thymus bouillon. The material of the thymus cells has been found to act in the reduction of the toxic properties of cultures of these bacilli, and further, by the action of thymus material on bacterial cultures products were obtained, which with

certainly protected 100 per cent. of the experimental animals, and the degree of toxine resistance could, when contrasted with the uninoculated animal, be expressed as 1000. No other means of protective inoculation appears so efficacious as this, since the most sensitive animals are rendered immune.

The question of inherited immunity has been the subject of much recent research. Doubtless at the present time the comparative immunity enjoyed by white races to certain infective diseases is probably to some extent due to inheritance, and this may be transferred either by the germ-cell or by the mother to the fœtus. The natural immunity which Algerian sheep possess against anthrax was shown by Chauveau (34) to be truly inherited and held by him to be due to the exceeding solubility of protective substances which were transferred to the fœtus. However, the rat when adult is exceedingly refractory to anthrax and other bacterial diseases, while young rats are susceptible. Fowls and pigeons are immune to tetanus and to anthrax, and Lazarus and Weyl (35) hold that this condition is inherited and not acquired, since after twenty-four hours of extra-ovular life chickens are found to be immune to the latter disease. The case is quite different with pigeons; the immunity is relative and not absolute as regards anthrax. The bacilli of this disease live in the tissues of these animals for as long as eight days (36), and while there increase in virulence, but adult birds do not succumb, while young pigeons can be easily inoculated (37). Even though living bacilli exist in the system they do not multiply, neither do the spores develop, and therefore in immune pigeons a bactericidal liquid cannot be the cause of the immunity.

The subject of inherited immunity has been dealt with by Ehrlich in several papers, in the earliest (38) of which a detailed account of his observations on ricin, abrin and robin is given. These bodies he regards as the toxalbumins of the seeds of *Ricinus communis* and *Abrus precatorius*, though S. Martin (39) has shown that the abrin isolated from jequirity seeds by Warden and Waddell (40) is a mixture of at least two proteids, a paraglobulin and a phyto-

albumose. He found that these bodies, as Stillmark (41) had shown was the case with ricin, possessed marked toxic properties which were wholly destroyed by boiling; the introduction of ricin by intravenous injection produces multiple thrombi, due to the clinging together of red blood corpuscles. By feeding mice with biscuits, to which ricin is added in known quantities, after a certain time, from one to two weeks, a condition of immunity to ricin injection is established, and this lasts for six to seven months. He further estimates the grade of immunity which is reached, by calculating that if 1 c.c. of a solution, 1 : 200,000 per 20 grammes body weight is the lethal dose of ricin, then if the animal withstands 1 c.c. of 1 : 500, then its immunity grade would be 400. In the blood of animals treated in this way and which are immune, or rather toxine-resistant, a body termed anti-ricin is present, and by the introduction of the serum of ricin-immune animals into others a relative degree of immunity is conferred. For robin (a toxalbumin from the bark of the acacia) the same statement holds good, and also for abrin; but the anti-bodies of any one will not annul a lethal dose of any of the other toxic bodies. A solution of abrin 1 : 100,000 is fatal for mice when 1 c.cm. per 20 grammes body weight is injected. By feeding with gradually increasing quantities of abrin these animals become highly immune, and this immunity can be inherited by the offspring. This condition might be due either to heredity in the ontogenetic sense or by the influence of hypothetical immunity-conferring bodies yielded by the mother directly to the foetus. In attempting to decide this matter it was shown by Ehrlich that the progeny of highly immune fathers and normal mothers showed no immunity, but were actually rather more sensitive than control animals, and therefore an idioplasm of the sperm is not capable of causing a transference of immunity, and, indeed, since the immunity was acquired, this result was to be expected. With immune mothers and susceptible fathers positive results were obtained, for as long as a month after birth a well-marked resistance to many times the lethal dose of abrin was evident. This resistance gradually diminishes

and by the commencement of the third month has disappeared, the protective substance no longer exists in the organism, and obviously this has been derived from antibodies of the mother. By pairing the offspring of parents which were resistant to abrin the succeeding generation was found to be as susceptible as normal animals, and therefore the ovum possesses no idioplasm capable of effecting a true heredity of the acquired immune condition. Apparently foetal immunity is an accepted fact for certain diseases and certain animals; but though this may play some part, Ehrlich's further observations showed that the protective, or anti-bodies, which are concerned in conferring immunity, are transferred by the milk. The passage into milk of drugs, such as iron (42), iodide of potassium, or garlic, is well established, and further, this fluid may not only contain micro-organisms which are pathogenic<sup>1</sup> or harmless (43), but, as Ketscher (44) has shown, goats protected against cholera yield milk which behaves like the serum of immune animals, since this fluid can render guinea-pigs refractory to a lethal injection of cholera bacteria, and this protective power was exerted when the protective material and cholera poison were introduced into different parts of the body; lastly, if the intoxication of cholera is already produced the milk possesses the power of abolishing this and curing the disease.

This important discovery of lactation immunity was conclusively proved by the susceptibility shown by the offspring of highly immune mothers which were suckled by a normal nurse and the immunity which followed when, conversely, offspring of susceptible mothers were suckled by an immune nurse. The degree of immunity also, as might be expected, since there is a transference of anti-bodies present in the milk, augments with the duration of lactation.

<sup>1</sup> The following observation is of interest. Nocard has shown that suckling goats easily succumb when anthrax bacilli are injected into the mamma by way of the lactiferous ducts. A goat rendered immune is unharmed by this proceeding, although the bacilli live within the gland for an indefinite period, and the milk is shown to possess virulent properties, since sheep inoculated with such milk die of typical anthrax.

It is consequently proved conclusively that even if there are any protective bodies in the offspring the quantity derived directly from the mother is almost nothing when contrasted with the amount yielded by milk. The protective substances which are in the milk exist also in the blood serum, since a normal susceptible mother is rendered immune and will furnish a protective milk when the serum of an abrin-resistant animal is introduced.

Transference by milk of substances which are antagonistic to the tetanus toxine also occurs during the lactation period. The protective serum of a horse was injected into a suckling mouse, and after twenty-four to seventy-eight hours this induced protection is found to exist also in the young, and in confirmation of the well-known results of Kitasato that tetanus when fully developed can be checked by introduction of protective serum, Ehrlich has found that tetanus developed in young animals can be absolutely arrested by feeding them from a highly immune mother.

Previous to these epoch-making experiments it was believed that the blood was the chief, if not the exclusive, vehicle of protective bodies, and the passage of these into the secretions was unknown. The mamma, however, is the only organ which secretes proteids to any extent, and it is remarkable that the anti-bodies, which are generally regarded as very easy of decomposition, are capable of passing through the bowels unchanged and then enter the body. Feeding experiments with the organs of immune animals never confers immunity.

In a later paper Ehrlich and Brieger (45) confirm the previous investigations. They find that the milk of a goat, which towards the end of pregnancy had been rendered immune to tetanus by daily injections of thymus-tetanus-bouillon mixture, which were slowly increased in strength, possessed a high protective value. The milk secreted by the animal showed, however, considerable fluctuations in strength, but injected into mice conferred upon these animals an immunity to inoculation with virulent tetanus cultures, which was at least sixteen times above that of the normal animal. Attempts to isolate the protective sub-



stances from milk were also made. This fluid was treated with 27-30 per cent. ammonium sulphate, and the first part of the precipitate was collected, dissolved in water, then dialysed, filtered and the filtrate evaporated *in vacuo* at 35°. 1 litre of milk yielded 1 gr. of a yellowish white, transparent substance which contained 14 per cent. of ammonium sulphate. This was shown by experiments to possess a value 400-600 times that of milk, in the whey of which the protective bodies are found. The later experiments of Brieger and G. Cohn (46) have yielded anti-toxines from milk which possessed an exceedingly high value in rendering animals immune from tetanus.

Experimental researches on the inheritance of immunity have also been made which seem to show that this inherited character may be transferred to the offspring by the egg or the sperm, and not wholly by the placental blood or the milk of the mother. The researches of G. Tizzoni and G. Cattani (47) show that the young of parents highly immune against tetanus possess a very definite resistance against the artificial production of this disease, though this is less than for the parents. These observers have also attacked the question of the possibility of the direct inheritance of immunity against rabies (48). The method consisted in pairing rabbits, *e.g.*, a resistant father with normal mother, and then testing the individuals of the litter. In three litters the first contained five individuals, and two out of these resisted repeated subdural inoculation of virus, and were still alive after seven months; two members of the second litter similarly treated were proved resistant, while all the third litter succumbed. Out of thirteen individuals only four survived inoculation with virus of great strength, which, without exception, always killed control animals. The conclusions drawn from these observations are that offspring can directly inherit the acquired immunity of the father, and that this by exclusion of other causes can only be due to transmission of the immune condition by the sperm. No peculiarities of the mother play any part in the results of the above experiments, since immunity occurs in individuals of two different litters



which had the same father. The immunity possessed by the offspring is less than that of the father, but unlike the immunity conferred by blood serum or milk this state is permanent.

A series of observations on the heredity of immunity have been undertaken by Gley and Charrin (49). Rabbits rendered immune to infection with the bacillus pyocyaneus were paired and the offspring tested. The experiments indicate that there is only occasional evidence of partial or absolute immunity. They consider that this is dependent entirely upon the male, for immune females tend to become sterile, and to produce immature or malformed offspring. In this they see strong evidence against accepting Weismann's theory of heredity.

Sufficient experimental work does not at present exist to permit of any definite attitude on this question of inherited immunity. Natural peculiarities, acquired characters and mutilations are apparently never transmitted, and the considerable literature which has grown up around this dogma leaves it absolutely uncontradicted. Certain diseases among white races, such as measles, small-pox and other inoculable diseases, seem to have lost something of their former virulence.<sup>1</sup> Yellow fever also is said to spare the negro and destroy the mulatto. In all these cases instead of a direct inheritance of susceptibility or of immunity it is at least possible that while receptive families have died out refractory families have succeeded in multiplying and maintaining their existence, and consequently have raised comparatively immune generations.

<sup>1</sup> Diseases such as small-pox, measles and syphilis were unknown among savage races until introduced by Europeans. For the marked susceptibility of savages see Bonwick, *Last of the Tasmanians*, and the *Black War of Van Diemen's Land*, 1870, and Moseley's *Notes by a Naturalist on the "Challenger,"* 1879, p. 341.

REFERENCES.

1. SALMON and SMITH. *Centralblatt f. Bac. u. Parasitenk.*, vol. ii., 1887.
2. WOOLDRIDGE. *Proc. Roy. Soc.*, 1887, p. 312, and Versuche über Schutzimpfung auf Chemischen Wege, *Archiv f. Anat. und Phys.*, *Phys. Abth.*, vol. iii., 1888.
3. WRIGHT. On Wooldridge's Method of producing Immunity against Anthrax by the Injection of Solutions of Tissue-Fibrinogen. *Trans. of Seventh Internat. Congress of Hyg. and Demog.*, vol. ii., p. 164, 1891.
4. NUTTALL. *Zeitsch. f. Hyg.*, vol. iv., 1888.
5. BUCHNER. *Centralblatt f. Bac. und Parasitenk.*, vol. v., p. 817, and vol. vi., p. 1, 1889.
6. HANKIN. *Proc. Roy. Soc.*, vol. xlviii., 1890; see also Ogata, *Centralbl. f. Bac. und Parasitenk.*, vol. ix., 1891; Tizzoni and Cattani, *ibid.*, vol. ix., 1891.
7. On Immunity. *Seventh Internat. Cong. of Hyg. and Demog.*, vol. ii., p. 147, 1891.
8. BUCHNER. Über Bacteriengifte und Gegengifte, Vortrag geh. im ärzt. Verein in München, am 7th Juni, 1893, *Munch. med. Wochensch.*, 1893, Nos. 24 and 25.
9. BRIEGER, KITASATO, und WASSERMANN. *Zeitsch. f. Hygiene*, bd. xii., 1892.
10. EHRLICH. Exp. Untersuch. über Immunität, *Deutsche med. Woch.*, 1891, No. 32.
11. BEHRING und WERNICKE. *Zeitsch. f. Hygiene*, bd. xii., 1892.
12. BEHRING und KNORR. *Zeitsch. f. Hygiene*, bd. xiii., 1893.
13. GIBIER. *Comptes Rendus*, 1882, t. xciv., p. 1605.
14. METSCHNIKOFF. *Virchow's Archiv*, 1884, bd. vii.
15. KANTHACK. *Brit. med. Journal*, 1892.
16. GOTTSTEIN. *Deutsche med. Woch.*, 1890, No. 24.
17. LEO. *Zeitsch. f. Hygiene*, 1889, bd. vii.
18. CHARRIN and ROGER. *Le Semaine med.*, 1890.
19. KÜLZ. *Pflüger's Archiv*, bd. xxiv., 1881.
20. GALTIER. *Lyon Journal*, 1892, p. 350.
21. HANKIN. *Trans. of Int. Cong. of Hyg. and Demog.*, 1891, vol. ii.
22. PENZO. *Centralblatt f. Bac. und Parasitenk.*, bd. x., 1891.
23. ROGER. *Le Semaine med.*, 1889.
24. VAILLARD et VINCENT, *Ann. de l'Inst. Pasteur*, 1891, No. 1, and Vaillard et Rouget, *ibid.*, 1892.
25. SANCHEZ-TOLEDO. *Le Semaine med.*, 1891, p. 261.
26. VAILLARD. *Le Bullet. med.*, 1891, p. 901.

27. WEICHELBAUM. *Wiener klin. Wochen.*, No. 33, 1893.
28. TIZZONI and G. CATTANI. Reference in *Baumgarten's Jahresbericht*, 1893.
29. TIZZONI and G. CATTANI. *Central. f. Bac. und Parasitenk.*, 1894, No. 9.
30. KANTHACK. *Central. f. Bac. und Parasitenk.*, vol. xii., 1892.
31. BENARIO. *Deutsche med. Woch.*, No. 1, 1894.
32. BRIEGER, KITASATO and WASSERMANN, see 9.
33. See 9.
34. CHAUVEAU. Influence de l'Inoculation de la mère sur la réceptivité du Fœtus, *Comptes Rendus*, 19 Juillet, 1880.
35. LAZARUS and WEYL. *Berlin. klin. Woch.*, 1892, No. 45.
36. SACCHI. Abstract in *Baumgarten's Jahresbericht*, 1893.
37. CZAPLEWSKI. *Zeitsch. f. Hygiene*, bd. xii., 1892.
38. EHRLICH. *Deutsche med. Woch.*, 1891, Nos. 32 and 44.
39. S. MARTIN. *Proc. Roy. Soc.*, 1887, p. 331.
40. Non-bacillar Nature of Abrus-poison. Calcutta, 1884.
41. STILLMARK. *Kobert's Arbeiten des pharmakol. Inst. zu Dorpat*, 1889, fasc. iii., p. 59. A résumé of his results is given by Gamaleïa, *Les Poisons Bactériens*, p. 73.
42. BISTROW. *Virchow's Archiv*, bd. xlv.
43. PALLESKE. *Virchow's Archiv*, bd. cxxx., 1893.
44. KETSCHER. *Comptes Rendus*, t. cxv., No. 18.
45. BRIEGER and EHRLICH. *Zeitsch. f. Hygiene*, bd. xiii., 1893.
46. BRIEGER and G. COHN. *Zeitsch. f. Hygiene*, bd. xv., 1893.
47. G. TIZZONI and G. CATTANI. *Deutsche med. Woch.*, 1892, No. 18.
48. G. TIZZONI and G. CATTANI. *Centralbl. f. Bac. und Parasitenk.*, 1893, vol. xiii., No. 3.
49. GLEY and CHARRIN. *Comptes Rendus*, t. cxvii., 1893.

GEORGE A. BUCKMASTER.

## EXPERIMENT IN MINERALOGY.

**I**T might appear unnecessary to call attention to the value of experiment in any branch of science; but we have to remember that at no very distant date mineralogy was formally divorced therefrom, and a complete reconciliation has never yet taken place.

In the first half of the present century, under the supremacy of the natural history school of Werner, the study of minerals was expressly confined to such features as could be examined by observation alone. In the words of Mohs, who may be regarded as the exponent of this school, "mineralogy is the natural history of minerals"; "natural history considers the natural productions as they are, and not how they have been formed"; "the natural-historical properties are those with which nature has endowed the bodies which it produces, provided those properties as well as the bodies themselves remain unaltered during their examination".

Nothing can be further removed from experimental science than this. In the light of present methods, some of the dicta of Mohs appear to a modern reader absolutely opposed to the spirit of progress. For instance: "It is very difficult to attain a correct knowledge of the productions of the mineral kingdom, if we confine ourselves to empiricism. Besides it is a waste of time, and the information thus acquired is at the best uncertain." If a person intends to acquire solid information in mineralogy he is recommended to "examine well-arranged collections which may be said to be useful only to those who wish to enlarge their information by observation and inquiry". "Properties which can only be observed during or after a change cannot be employed agreeably to the principles of natural history, and must therefore be excluded from mineralogy. Properties of this kind are: the fusibility of minerals examined before the blow-pipe; their solubility in acids; phosphorescence produced by heat; chemical analysis instituted to ascertain the quality or relative quantity of the component parts" (1).

It is difficult to believe that these were really the principles of the science little more than sixty years ago ; but, as a matter of fact, even before it had emerged from this Slough of Despond, systematic mineralogy was based upon experimental methods without which the chemical, physical and morphological characters of minerals cannot be determined.

The study of minerals, however, is no more limited to the determination of their characters than is the study of geology confined to the classification of fossils. A no less important branch of the subject is occupied with the investigation of their origin and the changes to which they are subject ; even here experiment is not a new thing ; as early as 1801 James Hall showed that chalk may be converted into crystallised calcite by heating it under pressure in a closed tube ; and after an interval of nearly a century the same methods and almost the same apparatus are being used in the synthesis of other minerals.

But there is yet another aspect of the subject which is the very life and essence of mineralogy if it is to exist as a science at all : namely, the discovery of the general laws of which the characters and changes of minerals are an expression ; the relations between their chemical, physical and morphological characters ; the molecular properties and structures which are to explain both their nature and origin.

In these matters, until recently, mineralogy was no more occupied with experimental methods than were sociology or astronomy ; and yet the mineralogist could not plead as an excuse that his materials were either too unwieldy or too distant to be brought within the scope of experiment.

Regarding chemical and crystalline structure, for example, numerous speculations exist ; but scarcely a single working hypothesis capable of any wide application ; the same is true of questions relating to the genesis of minerals.

The fact is that the science has experienced a temporary check owing to the want of experimental evidence by which the theories might be tested. Even the classification of minerals, the first and most important step, is at a stand-

still because the relations between isomorphous substances are but imperfectly understood. The present state of our knowledge on this subject is summarised in a valuable treatise recently published by Arzruni (2) as a section of Graham-Otto's *Lehrbuch der Anorganischen Chemie*; its application to mineralogy is to be found in the great treatises of Dana (3) and Hintze (4).

But reference to such books will only convince a critical reader of the necessity of further experimental research. Instance upon instance may be found in the very best explored regions of the science. The feldspars by all their characters declare themselves to be an isomorphous group, and we have therefore to harmonise the empirical formulæ  $\text{KAlSi}_3\text{O}_8$  of orthoclase and  $\text{CaAl}_2\text{Si}_2\text{O}_8$  of anorthite; but whether the formula of the latter is to be doubled and  $\text{CaAl}_2$  is to be supposed equivalent to  $\text{Si}_2$  in the former, or whether we are to suppose that  $\text{Si}_3\text{O}_8$  is a radicle which can replace  $\text{SiO}_4$ , is, without further evidence, a matter of the purest speculation; it is true that an appeal can here be made to the products resulting from the decomposition of feldspars, and the constitution formulæ generally adopted are based upon the kaolinisation of these minerals; in this connection reference may be made to a suggestive paper by Scharizer (5) on the metasomatic products of the silicates.

#### EXPERIMENTS ON CHEMICAL COMPOSITION.

A preferable method would be to investigate the action of various physical and chemical processes upon the mineral, in order to determine what proportions of its constituents are combined in different manners within the molecule. Very important in this respect are the numerous observations of Doelter upon the solubility of minerals and their behaviour in the presence of various solvents (6).

Particularly striking and promising among recent researches are those of Clarke upon the silicates, especially the mica group (7); the experiments were made to ascertain how far they conform to his view that such stable compounds as the natural silicates must be far less complex in constitution than is commonly supposed, and that they

may, in fact, be regarded as substitution derivatives of simple normal salts.

According to this view the mica group is derived from the normal aluminium silicate  $\text{Al}_4(\text{SiO}_4)_3$ , in which one or more atoms of aluminium are replaceable by other radicles.

Now Clarke has found that when serpentine is exposed to the action of *dry* hydrochloric acid gas, one-third of its magnesia is given up; from the fact that olivine is unattacked, while serpentine is attacked proportionally to the excess of oxygen over the orthosilicate ratio, he concludes that in the magnesian silicates, only that part of the magnesium is removed by gaseous hydrogen chloride which is present as the univalent group  $\text{MgOH}$ ; serpentine then is regarded as  $\text{Mg}_2(\text{SiO}_4)_2\text{H}_3(\text{MgOH})$ , which is a substitution derivative from the normal olivine orthosilicate  $\text{Mg}_4(\text{SiO}_4)_2$ .

Ripidolite gives up 13 per cent. of magnesia; if this be represented by  $\text{MgOH}$  the constitution falls under the type  $\text{R}''_2(\text{SiO}_4)_2\text{R}'_4$ , which is again an olivine silicate and brings the chlorites into the same series with serpentine.

On the other hand phlogopite is unaffected by gaseous hydrogen chloride, though completely decomposed by the aqueous acid; this is in accordance with the view that it is  $\text{Al}(\text{SiO}_4)_3\text{Mg}_3\text{R}'_3$ , a substitution derivative of normal aluminium orthosilicate.

The strength of Clarke's position as compared with that of other mineral chemists is that his arguments are based upon experimental evidence in addition to the ordinary analytical results. There is scarcely a single group of silicates for which some such evidence is not needed.

As another instance take the scapolite group; the nature of the scapolite series of minerals is evidently to be explained by the isomorphous intermixture of two or more substances; but the only available theory, that recently propounded by Tschermak (8), according to which they are mixtures of  $\text{Ca}_4\text{Al}_6\text{Si}_6\text{O}_{26}$  (meionite) and  $\text{Na}_4\text{Al}_3\text{Si}_4\text{O}_{24}\text{Cl}$  (marialite), is considerably weakened by the fact that the latter compound is purely hypothetical; the artificial production of this compound would of course immensely



strengthen the theory, and the same is true of the other numerous groups in which a hypothetical constituent is introduced.

Even in so well known a group as the amphiboles there is great doubt whether the aluminous varieties are to be explained by the replacement of one atom of Si by the univalent group  $\text{MgAl}$ , or whether  $\text{MgSiO}_3$  is to be regarded as replaceable by  $\text{RAl}_2\text{O}_4$ , or whether the metasilicate  $\text{RSiO}_3$  can form isomorphous mixtures with a silicate of the garnet type  $\text{R}_3\text{Al}_2(\text{SiO}_4)_3$ .

Or again take the variations of the optical characters in the pyroxenes—one of the very few groups which have been seriously studied in this respect—it is known that the extinction on a certain face, and the optic axial angle both increase with the percentage of iron, but various views are held on the nature of the variation; it was at first supposed that the increasing percentage of  $\text{Fe}_2\text{O}_3$  was attended by a regular change in the properties, but Doelter is of opinion that the increase is due to the simultaneous action of no less than three silicates which (with others) may enter into the composition of a pyroxene, namely,  $\text{CaFeSi}_2\text{O}_6$ ,  $\text{MgFe}_2\text{SiO}_6$ , and  $\text{MgAl}_2\text{SiO}_6$  (9).

In all these cases the production and study of artificial compounds is a great need; the laws which operate must obviously be more easily established upon pure substances of simple composition than upon the impure and complex compounds which occur as minerals.

The truth is that in whichever direction the mineralogist turns the problems by which he is confronted are precisely those which can only be solved by experiment; speculations exist in abundance, but they can only be confirmed or rejected by the decisive test of experimental research.

#### EXPERIMENTS ON CRYSTALLINE STRUCTURE.

One or two instances chosen from the crystallographic side of the subject will suffice to indicate how fruitful (though so rare) experiment has been in recent work.

It was a simple experiment by which Reusch converted

a crystal of calcite by mere pressure into two crystals united by a twin-plane; any one can repeat the experiment, as suggested by Baumhauer, by merely pressing a knife-blade into the edge of a calcite-rhomb, and the marvellous manner in which the part of the crystal which is pressed changes as though by magic to a new crystal must delight any who see the experiment performed; from this simple experiment have resulted modern conceptions of "gliding-planes" and "secondary twinning" produced in crystals by changes of temperature and pressure; this secondary twinning has now been produced in many substances and has been experimentally studied by Mügge; it has been observed in many minerals and is not without geological significance as indicating the former existence of pressure; it has moreover an important bearing upon theories of crystal structure, and has provoked the recent suggestive work of Lord Kelvin upon the "Molecular Tactics of Iceland Spar" (10).

Equally simple and striking is the experiment of Mallard upon boracite, a mineral which though apparently cubic exhibits double refraction; he found that when heated to  $265^{\circ}$  the crystals become isotropic; it is impossible to see this experiment without being led to inquire into the molecular structure which can explain so remarkable a phenomenon, and it has given rise to a flood of research.

Or take again that other experiment of Reusch, in which a number of mica plates are piled one above the other in the fashion of a spiral staircase; such a combination is found to rotate the plane of polarisation of a plane polarised ray of light just as it is rotated by a crystal of quartz; the experiment affords a striking justification of, if it did not actually prompt, the views of Sohncke and Mallard regarding the structure of quartz and other optically active crystals, according to which these crystals are composed of a spiral arrangement of particles (11).

Again it has generally been supposed that absolute repose is essential to the growth of well-developed crystals; in reality, however, direct experiments of Wulff have shown that under some conditions continual movement is an

advantage and not a hindrance, and need not therefore be excluded either in the laboratory or in nature (12).

#### EXPERIMENTS ON THE ORIGIN OF MINERALS.

But nowhere is the want of experiment more felt than in the question of mineral genesis.

The complaint used to be that experimental geology could scarcely expect success owing to our inability to reproduce the enormous pressures and temperatures which have prevailed during the natural production of minerals, and a still greater difficulty was supposed to be the great lapse of time required by the processes of nature.

In reality, however, these objections were many years ago removed by such discoveries as that of cassiterite in the antlers of deer in the Cornish tin works, of gold and crystalline pyrites in the woodwork of old mine-galleries, of crystalline zeolites in the masonry of the Roman springs at Plombières, and of minerals resulting from the decomposition of coins of comparatively recent date (13).

If the natural conditions can only be reproduced in the laboratory there is no reason why minerals which have in a score of centuries attained sufficient dimensions to satisfy the curators of museums should not be reproduced as microscopic crystals in as many weeks or even days.

Ebelmen, Sénarmont and Daubrée, to mention only a few of those who have occupied themselves with mineral synthesis, have prepared a large number of minerals in various ways; at first but little attempt was made to realise the conditions of nature, but by degrees higher temperatures and greater pressures were employed, until it became possible to reproduce many of the silicates which are characteristic of volcanic lavas and igneous rocks. These researches were prosecuted with much zeal by the French chemists to whom the development of mineral synthesis is mainly due, and one striking result of their experiments has been to demonstrate the important part played by such elements as chlorine, fluorine and nitrogen, even though they do not enter into the composition of the final product.

A recent achievement in this direction has been the manufacture of crystalline sapphire and ruby, by Haute-feuille, Frémy and Verneuil (14).

Finally we may notice some recent work which illustrates both the value and the need of experiment in connection with the genesis of certain minerals which are found associated with basic rocks; that is to say with igneous rocks containing less than 55 per cent. of silica.

Among those minerals whose origin is shrouded in the greatest mystery are platinum and diamond, which, like several of the gems, are for the most part found in gravels and river washings, and not in the original matrix.

Some quite recent observations have contributed much to a better understanding of their origin.

In the first place Inostranzeff has found platinum actually disseminated through a rock consisting mainly of chromite and serpentine (15), that is to say an altered basic rock of which the metal appears to have been originally a constituent; with this discovery may be compared that of a nickeliferous iron in serpentine from New Zealand; this has been described by Ulrich under the name Awaruite (16).

Nickel-iron was formerly supposed to be exclusively meteoric, but the large masses brought by Nordenskiöld from Ovifak in North Greenland have been proved to be metallic concretions formed in basalt and not of meteoric origin (17).

Here then are three instances of metallic segregations which have solidified from basic igneous rocks.

Somewhat similar may be the history of the diamond; various occurrences of diamond in a natural matrix have been reported, but they have always been somewhat dubious; only in the South African workings at Kimberley is the occurrence of the gem difficult to explain on any other hypothesis than that it has actually crystallised from the serpentinous rock in which it is found. This, which is a basic igneous rock known by the name of "blue ground," fills vertical pipe-shaped shafts of unknown depth, and the diamonds which are dispersed through it bear all the

familiar tokens of crystallisation from a solvent ; they have sometimes rounded edges and sharply defined etched figures, characteristic of an incipient corrosion by the solvent ; an octahedron of alum during crystallisation becomes covered with etched triangles precisely resembling those of the diamond the instant a rise of temperature occurs.

On the other hand the "blue ground" has the appearance of occupying a volcanic vent, and contains fragments of so many other minerals and rocks that it is rash to assert that the diamond may not have been, like them, caught up elsewhere by the molten mass.

The resemblance between basic terrestrial rocks and meteorites has been frequently pointed out ; there is a regular gradation from the acid igneous rocks through the more basic to the felspathic meteorites (which have much the same composition as the basaltic rocks), while lower in the series come the olivine and iron-bearing meteorites, ending with meteoric iron as the extreme limit.

Now a recent very striking discovery is that of a meteoric iron containing diamond ; the occurrence was announced by König (18), and the iron was found in 1891 at Cañon Diablo in Arizona. Minute particles supposed to be diamond had previously been observed in the meteoric stone which fell at Nowo-urei in Russia in 1886.

König's determination has been subsequently confirmed by the French observers Mallard and Friedel.

Various forms of carbon had been known to exist in meteoric irons and it had been suggested that some of these were altered diamond, but this substance itself had not been previously found in a meteoric iron.

It is natural to conclude that the diamond has crystallised from solution in the molten metal.

Moissan has lost no time in putting this idea to a practical test with the help of the high temperature attainable by means of the electric furnace (19). He finds that, with the addition of great pressure, he is able to dissolve carbon in iron, silver and certain alloys, and that it reappears from the solvent in the form both of

diamond and carbonado (a black amorphous modification similar to that found in Brazil and used for rock drills).

It is interesting to note in this connection that Norden-skiöld had observed one piece of the Ovifak iron to be so hard that it could not be cut or worked, and in view of the constitution of the Cañon Diablo meteorite it seemed possible that this might also contain diamond; it was examined by Moissan, who found no diamond, but an equally interesting result was obtained, for the iron was found to contain sapphire, to which no doubt the hardness is due (20).

Taking all the above observations into account, it is more than probable that the blue ground of Kimberley may be the original matrix of the South African diamonds.

Now a recent experiment tends to confirm this view; it has not only been found that microscopic diamond, graphite and carbonado are disseminated through the blue ground, just as they are in the molten iron of Moissan's experiment; but further, that under the influence of high temperature and great pressure the blue ground itself may be made to corrode, to etch and to redissolve the diamond (21).

The general tendency of recent research is to suggest that several other metals and metallic compounds whose origin is particularly doubtful may have crystallised out of basic igneous rocks. These very questions have attracted much interest among petrologists who have endeavoured to ascertain how rocks of varying composition have solidified from one and the same subterranean magma by a process of successive segregation.

Vogt has approached the subject more from the mineralogical and metallurgical point of view. Two years ago he showed that in all probability the iron ore deposits of Ekersund and Taberg have been separated by concentration from basic igneous rocks. In the Ekersund-Soggen-dal district the ore is an ilmenite-norite dyke, occurring in a labradorite rock; at Taberg the ore is a mixture of titaniferous magnetite with olivine and a basic feldspar, which is a concentration patch in an olivine-hyperite (22).

In a remarkable paper published in the new *Zeitschrift für praktische Geologie* he has extended these views to the nickel ores, and has shown that the nickeliferous sulphides in many parts of the world have probably been concentrated in a similar manner (23). At Esteli in Norway, Klefva in Sweden, Varallo in Piedmont, and Sudbury in Canada, nickeliferous pyrrhotite associated with copper pyrites, ilmenite, etc., is the ore, and it occurs in gabbro (norite).

(In connection with what has been said above, it is interesting to note that some of the Sudbury nickel ore is platini-ferous, and that an arsenide of platinum has been found in the district (24).)

The well-known nickel ores of New Caledonia are mostly silicates, and are associated with chalcedony, brucite, magnesite and other alteration products, but here also they occur in serpentine, *i.e.*, in an altered basic rock from which again the nickel may have been derived by concentration. Vogt himself, however, does not incline to this opinion.

These and similar views regarding magmatic concentration, which are rapidly finding acceptance among geologists and petrologists, are referred to here as examples both of the value of experimental evidence and of the need of it. The order in which minerals crystallise from a siliceous magma and the manner in which certain elements unite to form definite minerals have been verified by numerous experiments with slags, and it is this that invests Vogt's views upon the concentration of the oxides with a special value. As regards the sulphides and much of the purely petrological speculation, the experimental evidence is still wanting.

On the mineralogical side the subject has considerable practical importance; for it may lead to a better knowledge of the distribution not only of metalliferous ores but also of the rare elements which, without doubt, do exhibit a tendency to congregate in certain limited areas.

From every point of view, experimental mineralogy is a subject which has always been strangely neglected in England.



## BIBLIOGRAPHY.

1. F. MOHS. Treatise on Mineralogy (trans. by W. Haidinger). Edinburgh, 1825.
2. A. ARZRUNI. Physikalische Chemie der Krystalle. Braunschweig, 1893.
3. E. S. DANA. A System of Mineralogy (sixth edition). New York, 1892.
4. C. HINTZE. Handbuch der Mineralogie (in course of publication). Parts i.-vii. Leipzig, 1889-93.
5. R. SCHARIZER. *Zeitschrift für Krystallographie*, xxii., p. 369.
6. C. DOELTER. Allgemeine Chemische Mineralogie. Leipzig, 1890.
7. F. W. CLARKE and E. A. SCHNEIDER. *American Journal of Science*, xl., p. 303, etc.
8. G. TSCHERMAK, *Mineralogische und Petrographische Mittheilungen*, vii., p. 400.
9. C. DOELTER. *Neues Jahrbuch für Mineralogie*, 1885 (i.), p. 43.
10. Sir W. THOMSON. *Comptes Rendus*, cix., p. 333.
11. L. SOHNCKE. *Zeitschr. f. Krystallographie*, xix., p. 529.
12. L. WULFF. *Zeitschr. f. Krystallographie*, xi., p. 120.
13. S. MEUNIER. Les Méthodes de Synthèse en Minéralogie. Paris, 1891.
14. E. FRÉMY. Synthèse du Rubis. Paris, 1891.
15. A. INOSTRANZEFF. *Comptes Rendus*, cxvi., p. 155.
16. G. H. F. ULRICH. *Quarterly Journal, Geological Society*, xlv., p. 619.
17. K. J. V. STEENSTRUP. *Mineralogical Magazine*, vi., p. 1.
18. See A. E. FOOTE. *American Journal of Science*, xlii., p. 413.
19. H. MOISSAN. *Comptes Rendus*, cxvi., p. 218.
20. H. MOISSAN. *Comptes Rendus*, cxvi., p. 269.
21. W. LUZI. *Berichte d. Deutschen Chemischen Gesellschaft*, xxv., p. 1470.  
H. MOISSAN. *Comptes Rendus*, cxvi., p. 292.
22. J. H. L. VOGT. *Geologiska Föreningens i Stockholm Förhandlingar*, xiii., p. 476.
23. CLARKE and CATLETT. *American Journal of Science*, xxxvii., p. 372.
24. WELLS and PENFIELD. *American Journal of Science*, xxxvii., p. 67.

H. A. MIERS.

## ALGÆ.

STUDENTS of phycology hope so much from the successive parts of Engler and Prantl's *Pflanzenfamilien* that its progress is watched only less critically than the necessary *Sylloge* of De Toni. After the depression produced by Wille's uncritical and often inaccurate treatment of the *Chlorophyceæ*, Kjellman's excellent account (1) of the olive and brown Algæ has been very welcome. He has set about his work in a very exhaustive fashion on the whole, and has skilfully assembled his orders and their genera with the experienced eye and judgment of one who knows most of them at first hand, and he has above all furnished an abundance of clear illustrations. It is very gratifying to observe that the more obscure the group, the more anxiously accurate is its treatment. It is difficult to refrain from apparently exaggerated words of praise of all this excellence, and one says this the more readily that there is a complaint of some gravity to be made. Dr. Kjellman has, doubtless unconsciously, ignored much of our native work at these orders done during recent years, and the result is not only casual imperfections, but, at all events, one omission of an ordinal type. He retains *Splachnidium* among the *Fucaceæ*, though nearly two years have elapsed since its removal to an order of its own for reasons of undisputed validity, of which he does not appear to have heard. There is similar ignorance of other papers by other writers, in other journals, all British, and I am not complaining of mere trivialities, but of a neglect of British work which is not confined by any means to Dr. Kjellman, or to this subject. It is far too prevalent among continental botanists, and contrasts painfully with the exaggerated respect frequently paid to their opinions among ourselves. I should like to point to the excellent figures of *Fucaceæ* and *Laminariaceæ* and of genera especially that are known in this country only to students in our great herbaria. In this and in his treatment of the boreal forms which Dr. Kjellman knows so well from his

experiences on the "Vega" and other expeditions, he has shown such good judgment that one is almost inclined to forget all complaints. Accessible figures of such Laminarian genera as *Cymathere*, *Ulopteryx*, *Postelsia*, *Thalassiophyllum*, *Agarum*, *Costaria*, *Dictyoneurum*, all within one book, is a boon to all students who are beyond range of excellent libraries.

Mr. Setchell's previous work has been so thoroughly good, and his study of the Laminarian *Saccorhiza* so noteworthy in this respect, that one could scarcely wish a difficult task like this (2) in other hands. There is hardly a group of Algæ that surpasses the *Laminariaceæ* in the amount of interest taken in them; and since no one has attempted a general classification of the order since J. G. Agardh in 1848, with the exception of the contemporary Kjellmanian account cited above, there was an urgent need for such a paper as this one. In addition to the discussion of their distribution, he gives an account of the genera and a systematic synopsis of them. I observe that *Adenocystis* is left out, but from my examination of Hooker and Harvey's typical specimens, I doubt the wisdom of this. He gives a valuable table of the distribution of all the species in defined areas. One cannot but rejoice that Mr. Setchell has had the courage to "lump" species in so satisfactory a way. For example, he properly recognises only one species of *Macrocystis*, viz., *M. pyrifera*. There are still too many species of *Laminaria* and of *Alaria*, especially the latter, founded on the most trifling grounds. No doubt they will follow their defunct allies of *Macrocystis* when the order is monographed. I observe only one omission of interest, viz., *Laminaria Schinzii* Foslie, which enters the southern tropical Atlantic at Walfisch Bay. A very satisfactory aspect of this paper is that it gives botanists a claim on Mr. Setchell to monograph the order now that he has put his hand to the plough.

Prof. Johnson describes (3) and figures an interesting new species, *Pogotrichum hibernicum*, in a short paper. He gives us a detailed comparison of *Litosiphon*, Harv., and *Pogotrichum* Rke. In the course of his corre-

spondence with Prof. Reinke, he has extracted the admission "that had he known of the Kilkee plant [*i.e.*, *P. hibernicum*], he would have hesitated before founding the genus *Pogotrichum*". Prof. Johnson himself comes to the conclusion: "Thus I am led to believe that the two genera, *Litosiphon* and *Pogotrichum*, are one and the same, and ought to be united, and that *L. Laminariæ* and *P. hibernicum*, if not one species, are very closely allied". This is a very diffident attitude towards the genus he has just been adding to, and phycologists who read Prof. Johnson's detailed reasons will regret that he has not had the courage of his opinions to take "a short way with" *Pogotrichum* after disabling it.

Miss Barton has, with much industry and care, brought together the records of seaweeds from the Cape (4), and with the help of collections made by Messrs. Boodle, Scott Elliot, Tyson and others, principally in the British Museum, very largely increased these records. The list does not claim to be more than provisional, and to be inclusive rather than exclusive in its tendency—very wisely in the present state of our knowledge—but it furnishes material for an interesting, if short, essay on the geographical relations of the Cape marine flora. There is a table of detailed comparisons of the Cape seaweeds with those of Australia, of Western Australia only, and of Kerguelen Land—and another table of comparisons with the warm Atlantic and the Indian Ocean. The latter table appears also in the last paper cited under (5), of which, with the other papers under the same number, it will become me to give only a colourless abstract. The writer there uses the Cape totals furnished by Miss Barton to make more effective his comparison between the marine floras of the warm Atlantic and Indian Ocean. "We have here two tropical marine floras cut off from each other by a permanent continental area, and communicating only *via* the Cape. That these floras have been periodically mingled at the epochs of warmer climate at the Cape seems a reasonable conclusion with regard to a group of such antiquity as the Algæ, and the proportions of species in common and genera in common

between the different regions, and among all three may have a significance in this respect to students of distribution." The writer finds that the genera of the tropical areas are largely the same while the species are in a high proportion different. This is particularly marked in the case of such a tropical and subtropical order as the *Siphonæ* (*sensu* Agardh). There are twenty-three genera of this order in the warm Atlantic and sixteen in the Indian Ocean, and the whole of the sixteen are genera in common; while only twenty-nine species are possessed in common out of the two totals of ninety-nine and seventy-two, though the waters of the Cape are now warm enough to sustain such generic types as *Caulerpa*.

Of the other papers cited under (5) the first is a continuation of the study of the morphology of the *Fucaceæ*, especially their conceptacles, which was initiated by Bower, and carried further by Oltmanns. The generic types dealt with are mostly from remote places, and perhaps the most interesting is *Notheia*, by Miss Mitchell, though the nature of the material did not suffice for a complete study. Its interest is mainly that it appears to be a much degraded, truly parasitic Fucaceous genus. The second paper, by Miss Whitting, describes a new endophytic Alga *Chlorocystis Sarcophyci*, which inhabits the fronds of *Sarcophycus*, and appears to be most nearly related to the interesting form described some years ago by Dr. Perceval Wright, as *Chlorochytrium Cohnii* occurring in various Algæ in our own seas. The next paper by the present writer is a study of *Halicystis* (a genus new to Britain) and *Valonia*, of which latter genus the mode of reproduction is described. In her paper on *Hydroclathrus* Miss Mitchell describes the vegetative and reproductive structure of a singular type, and in the following paper the present writer gives an account of his examination of the cryptostomata (fasergrübchen) of three genera of *Laminariaceæ* and compares their development, etc., with those of the *Fucaceæ* and *Splachnidiaceæ*, and ventures certain speculative views as to the significance of these puzzling structures.

Dr. Schütt gives (6) a valuable account of the results

of the German Plankton Expedition, so far as they concern the Algæ of the open ocean, prefaced by an essay on the general character of such a flora and the conditions of its existence. The expedition has not added very greatly to the number of pelagic Algæ, nor has it introduced any new types. It also failed to find both Coccospheres and Rhabdospheres, and consequently to furnish material for advancing our knowledge of the most puzzling denizens of blue water. Dr. Schütt, in devoting a few lines to this subject, appears to favour either of the views, that they may belong to the *Foraminifera*, or that they may be inorganic formations. This is sinning against the light; but in any case little value need be attached to his opinion on this subject, since his acquaintance with the objects is, like his views, second hand. He records *Halosphæra viridis*, hitherto known as a surface organism, from "between 1000 and 2200 m."—a remarkable find of a green alga in regions of darkness, to which, however, we may presume it was swept by the movements of water currents. The valuable portion of the book consists of the estimates of volume of the constituents of the pelagic flora. Though no new broad fact affecting our knowledge of the general distribution of the pelagic Algæ emerges from the present employment of this method of estimation, it is plainly a good method, and after more extended use will give increase of knowledge.

The extensive work of Prof. Schmitz of Greifswald, in preparation for his forthcoming book on the *Florideæ*, has been so eagerly and conscientiously performed, as exhibited in a series of short papers the most recent of which are grouped under (7), that no student can fail to admire it. So far as his system of the *Florideæ* has been disclosed to us, it is distinguished by the special weight he has attached to very minute characters, and in some minds there is a misgiving that this weight is of undue gravity, since it appears to exclude characters of greater prominence, but possibly less stability—that, in short, there is some danger of his system tending towards an artificial one. There may be something in such a misgiving, and certainly characters are none the better for being minute, but from intimate know-

ledge of Dr. Schmitz's methods, and of his published work, I think those who take this adverse view are at all events not justified in their fears by the past, and ought to reserve them until the publication of Dr. Schmitz's book. No one can deny his extraordinary skill and sound judgment in the discrimination of obscure forms, and most British phycologists are personally indebted to him for the exercise of these gifts. In his *Kleinere Beiträge* the most interesting of the short papers is a discussion of the systematic position of the *Bangiaceæ* called forth by Prof. Johnson. In the first cited of the papers on genera of *Florideæ*, that devoted to *Lophothalia*, Dr. Schmitz disentangles a peculiarly difficult systematic puzzle and founds four new genera, *viz.*: *Wrightiella*, *Murrayella*, *Lophocladia*, and *Wilsonæa*. He clears up a like obscurity in his paper on *Microthamnion* J. Ag. = *Seirospora* Harv. Dr. Heydrich, whose paper I have placed next, also describes a new genus of much interest with Schmitzian precision.

To return to Dr. Schmitz's studies of genera, the most interesting of all is his paper on *Actinococcus*, in which he engages in a polemic with Reinke. The subject is the existence or not of this vexed genus. Schmitz in his list of genera of *Florideæ* records *Actinococcus* as a good genus, and Reinke in his *Algenflora der westlichen Ostsee* recognises it also on the ground of letters received from Schmitz. Now, however, Reinke has become doubtful of the independence of *Actinococcus*, and, as he puts it, "in agreement with the majority of phycologists" is inclined to see in this genus only the nemathecium of *Phyllophora Brodiaei*. This was certainly a daring deed of Reinke, since on just such a point as this I fancy most phycologists would consult their safety by agreeing with Schmitz, in whose particular line of work the matter certainly comes. Dr. Schmitz exhibits talents of debate as well as resources of knowledge in the discussion, and the majority of phycologists, wherever they may have stood before, must now be convinced. The phrase about this "majority" evidently has rankled and has borne fruit in a return compliment about "ein elegantes Bilderwerk" and "elegante Tafeln," which admirers of Reinke's



*Atlas* will know where to place. Such things may be sad, but they relieve the tedium of long German papers!

Mr. Buffham's painstaking work (8), so modestly set forth, is in continuation of previous discoveries of the same kind. British phycology is much indebted to him for this quiet building up of gaps in our knowledge of the *Florideæ*, and especially of their antheridia.

The study of *Caulerpa prolifera*, by Dr. Klemm (9), is so much more physiological than phycological that I need do little more than mention its existence here. Incidentally he upholds the view that the trabeculæ serve principally to maintain the external form of the organs of *Caulerpa* when in a turgescient condition. This is the view generally ascribed to Janse of late years, but of course it has always been every one's view more or less, except Noll's. The latter thinks that this is one of the least important of the uses of the trabeculæ, which he regards as serving the plant in the conduction of dissolved substances, contending that turgor itself takes care of the plant's stability. Dr. Klemm's research is mainly concerned with a partial study of the causes of form development. The genus affords a magnificent field for such study, since it contains species resembling in their outward appearance most of the characteristic types of vegetation. We shall all be much better acquainted with the forms of this extraordinary genus when Mrs. Weber van Bosse has completed her monograph of it now in progress.

Dr. Lagerheim's interesting paper (10) on *Rhodochytrium*, a new genus he has discovered inhabiting a composite, *Spilanthus*, in Ecuador, favours the view that the *Chytridiaceæ* are allied to the *Protococcaceæ*, rather than to higher groups of Fungi. *Rhodochytrium* is certainly a type of interesting life-history, but it does not appear to bring *Protococcaceæ* and *Chytridiaceæ* morphologically any nearer than the species of *Chlorocystis* investigated by Prof. Perceval Wright, Miss Whitting and others. However, it is a fresh instance and a fresh confirmation of an opinion now shared by many cryptogamists. Lagerheim thinks it not improbable that *Rhodochytrium* possesses no chlorophyll and that the chlorophores are reduced to leucoplasts. Starch

is abundantly present, particularly in the resting sporangia. The red colouring matter occurs in the form of oil drops, and the colouring substance itself he thinks is hæmatochrome or, at least, something nearly related to it. Though this might be considered indicative of the presence of chlorophyll, it is to be remembered, as Lagerheim states, that this substance (or something like it) occurs in Fungi which have no chlorophyll, *e.g.*, the *Uredineæ*, *Chrysochytrium*, etc. Dr. Lagerheim does not appear to have attempted to reduce the hæmatochrome by experimental cultivation, and thus disclose the presence or absence of chromatophores, as Schmitz successfully did in the case of *Hæmatococcus*, *Chroolepus*, etc. One feels at first inclined to scout relationships on physiological grounds such as this link would establish, but it is only fair to remember that after all many of the differences between *Protococcaceæ* and *Chytridiaceæ* are merely physiological.

I must content myself with a mere chronicle of Dr. Klebahn's paper (11) on genera of lower Algæ. It is a valuable one, but it hardly lends itself to a brief account from its critical systematic character. This admirable monograph (12) of the homocystal *Nostocaceæ* is the sequel to the *Revision des Nostocacées Hétérocystées* by Bornet and Flahault, which appeared a few years ago. It bears all the external marks of supreme care in the text and beauty of illustration that Bornet and Thuret have set example in, and, when the book is put to the test of use, it fails in no way to come up to the same high standard in its solid excellence of workmanship. In order to be in a proper spirit and condition of mind to appreciate this monograph, one must have tried to name *Oscillariæ*, and to arrange a collection of them without it. The condition of the group was chaotic, and it is now well ordered. M. Gomont has conscientiously investigated the claims to stability of a vast number of types, and has done this part of the work—the most valuable—in a way indicated by the lists of *species excludendæ* and *species inquirendæ*, almost as much as by the positive evidence of the proper part of the monograph—its species and synonymy. The division of the genera into sections is very judiciously

done, and most helpful to those who work with the book. One cannot help lamenting that *absolute* as well as relative measurements of size should be held to be a character—and the fashion is spreading into other departments of cryptogamic botany. One knows how disastrously it has worked in species-making of Diatoms (which may vary to the extent of half their size), and how deadly a weapon it proves in the hand of a rabid species-maker; but in the present case no one can blame M. Gomont for any abuse of the character of absolute size—it is in fact kept to a strictly subordinate value. M. Gomont has merited unreserved congratulations.

The papers grouped under (13) are systematic, and deal with the marine Algæ of the Scandinavian shores of the North Sea and its basins, and our own coasts as well. They are all of a character to interest students of British phycology, since the Scandinavian Algæ, when not identical with our own, are very closely allied. Major Reinbold's marine flora of Kiel Bay is concluded in the part cited, and we now have a critical account of the region that yielded many of the interesting plants of Reinke's *Atlas deutscher Meeresalgen*. Major Reinbold has done it exceedingly well, and his discrimination of species is the work of an acute and enthusiastic specialist. The same remark applies to Foslie's study of the Norwegian forms of *Ceramium*, a genus of heart-breaking tendency to vary. The students of British *Ceramia* will find it interesting enough to provoke criticism, no doubt, and though there are "crowns to be broke" over such matters, the contest needs an audience of specialists. The two papers by Dr. Gran and the notes by Mr. Batters represent useful work, and it may not be out of place to urge Mr. Batters onwards with that systematic account of the British marine Algæ which he is engaged upon, and so many workers are waiting for. Such notes as he furnishes in *Grevillea* only whet the appetite for the complete book.

There have been very few "published sets" of Algæ (14) recently, but Mr. Holmes' *fasciculi* are always welcome since they represent his industry in the study of the British marine forms. Much the best of all published specimens of Algæ are Wittrock and Nordstedt's fresh-water sets, and no

less than four of these have recently appeared to atone for a dormant period.

The complaint has to be made that *marine* published *fasciculi* (of several authors) are too exclusively European with the single exception of the admirable series published by Messrs. Farlow, Eaton & Anderson. If the collectors at the Cape or in our Australasian colonies or in the China seas could be induced to follow such an excellent example, it would have a stimulating effect on the study of phycology in Europe, by distributing types now found only in large collections like the British Museum, Kew, Dublin, Harvard and Paris.

#### BIBLIOGRAPHY.

1. Die natürlichen Pflanzenfamilien von A. Engler und K. Prantl (Lief. 86 and 97 containing orders of *Phæophyceæ*, by F. R. Kjellman, 1893).
2. On the classification and geographical distribution of the *Laminariaceæ*, by William Albert Setchell (*Trans. Connecticut Acad.*, vol. ix., 1893).
3. *Pogotrichum hibernicum* n. sp., by T. Johnson (*Scient. Proc. Roy. Dubl. Soc.*, vol. viii. N.S., part i.).
4. A provisional list of the Marine Algæ of the Cape of Good Hope, by Ethel S. Barton (*Journal of Botany*, 1893).
5. *Phycological Memoirs*, edited by George Murray. Part ii. containing notes on the morphology of the *Fucaceæ*, by A. Lorrain Smith, E. S. Barton, M. O. Mitchell, F. G. Whitting; on *Chlorocystis Sarcophyci*, a new endophytic Alga, by F. G. Whitting; on *Halicystis* and *Valonia*, by George Murray; on the structure of *Hydroclathrus*, by M. O. Mitchell; on the cryptostomata of *Adenocystis*, *Alaria* and *Saccorhiza*, by George Murray; a comparison of the marine floras of the warm Atlantic, Indian Ocean, and the Cape of Good Hope, by George Murray.
6. Das Pflanzenleben der Hochsee, von Dr. Franz Schütt (Ergebnisse der in dem Atlantischen Ocean ausgeführten Plankton Expedition der Humboldt Stiftung). Kiel und Leipzig: Lipsius and Tischer, 1893.
7. Kleinere Beiträge zur Kenntniss der Florideen (*Extr. La Nuova Notarisia*, 1892-93). Die Gattung *Lophothalia* and Die Gattung *Microthamnion*, von Fr. Schmitz. *Pleurostichidium*,

- ein neues genus der Rhodomeleen, von F. Heydrich (*Ber Deutsch. Bot. Gesellsch.*, bd. xi., 1893). Die Gattung *Actinococcus*, von Fr. Schmitz (*Flora*, 1893).
8. On the antheridia, etc., of some *Florideæ*, by T. H. Buffham (*Journ. Quek. Micr. Club*, vol. v., ser. ii., 1893).
  9. Ueber *Caulerpa prolifera*; ein Beitrag zur Erforschung der Form—und Richtkräfte in Pflanzen, von Paul Klemm (*Flora*, 1893).
  10. *Rhodochytrium* nov. gen. eine Uebergangsform von den Protococcaceen zu den Chytridiaceen, von G. de Lagerheim (*Bot. Zeit.*, 1893).
  11. Zur Kritik einiger Algengattungen, von H. Klebahn (*Pringsheim's Jahrb.*, bd. xxv., heft 2, 1893).
  12. Monographie des Oscillariées, par Maurice Gomont (*Extr. Ann. Sci. Nat.*). Paris: Masson, 1893.
  13. Die Algen der Kieler Föhrde, by Th. Reinbold (*Schriften d. Naturwissensch. Vereins für Schleswig Holstein*, bd. x., 1893). The Norwegian Forms of *Ceramium*, by M. Foslie (*Det Kgl. Norske Videnskab. Selsk. Skrifter*, 1893). En Norsk form af *Ectocarpus tomentosoides* and Alge vegetationem i Tonsbergfjorden, af H. H. Gran (*Christiania Videnskab. Selsk. Forhandl.*, 1893). New or critical British Algæ, by E. L. Batters (*Grevillea*, 1893).
  14. Algæ Brit. Rar. Exsicc., *Fasc.* vi., Nos. 126-150, by E. M. Holmes. Algæ Aquæ dulcis exsiccatae. *Fasc.* xxii.-xxv., Nos. 1000-1200, by Wittrock and Nordstedt. Stockholm: Marcus, 1893.

GEORGE MURRAY.

## JOTTINGS FROM RECENT NEUROLOGICAL PROGRESS.

WHEN viewed across a sufficient interval of years the chief advance in the neurological knowledge of the century with whose last decade we now move will likely enough be held to lie among facts that find but scanty place in the physiological annals of the time. If by *hypnosis* we understand all that is really true in the domain of mesmerism, animal magnetism, and the like, few discoveries in neuro-physiology can take rank beside the revelation of the power of "suggestion" and of the manifestations obtainable from the nervous system by direct or indirect play on its "suggestibility". Through these loom nearer the approaches to a vantage-ground whence may be possible a less cramped survey of those reservoirs and channels, which, to adopt a metaphor from Hughlings Jackson, occupy the highest altitudes of nervous conformation.

In other fields of neurology, where science starting earlier has fared further, a soil less virgin bears a growth less rapid, if at the same time less rank. The harvest yields at least abundant seed for present sowing. Physiological research is not of nature finite in the sense of ever reaching a true end. There are chosen by the workers more or less arbitrary halting-places; from these, in glancing back at the thing done, they see most clearly the manifold next to do. A "completed" research, unlike the just read novel, begets desire to take it up again. The record, even if not nutrient, is stimulant; but the recently "completed" researches, to inadequate consideration of which the following few pages are given, can well lay claim to both the attributes.

Just prior to the discovery by Fritsch and Hitzig of an excito-motor region in the cortex of the brain Goltz had

succeeded (1869) in demonstrating by excellent experiments that in the frog many reactions commonly ascribed to the highest nervous centres, *i.e.*, the cerebral hemispheres, are really referable to lower (*e.g.*, bulbo-spinal). These latter remain competent for the reactions even when the higher have been eliminated from the problem altogether by absolute removal. The scope of this theme Goltz proceeded to extend to mammalian physiology. He studied in mammals the intrinsic powers of the spinal cord in its lowest third, that being the portion most readily isolable from all higher centres. The results obtained were richly instructive. They revealed a plenitude of independent spinal function hardly surmised before, still less admitted as doctrinal. Some wide differences lay between the phenomena observed in the amphibian and the mammal. One of these consists in the deep prolonged depression of function, which in the latter immediately succeeds infliction of the tranma (*e.g.*, severance of the spinal cord). In Goltz's terminology "shock" is much greater in the mammal, more inhibitions are set up and they subside less soon. Minutes in the frog become in the dog days. With faith that the two species, though far apart in the vertebrate scale, are both exponents of the same radical principles of action, driving, it is true, a system more complex in one case than in the other, Goltz finally, in 1875, began an attempt to determine the possibilities of the mammalian bulbo-spinal axis (including cerebellum) as a separate whole apart from cerebral hemispheres altogether. The reactions of the dog without cerebrum were to be studied as had been those of the frog. Great experimental difficulties have lain in the way; but at last Goltz has been in a position to place on record, eighteen months ago, observations carried out on dogs existing for long periods without cerebrum.<sup>1</sup>

A dog without cerebrum moves, sits, rises or walks unhindered by noticeable paralysis; he is indeed prone to wander restlessly, and in his course takes heed of obstacles



and avoids them. At night he sleeps, curled up as is the mode with normal dogs. To awake him a loud sound, *e.g.*, the bray of a bicycle horn, is requisite. It is easier to awake him by a pat on the flank, and to this, if repeated, he soon answers with a growl. When awake, if one of his feet be taken he tries to escape much as a normal dog will try, but somewhat awkwardly; if not released he barks angrily and turning his head bites at the hand holding him, though clumsily missing his object sometimes widely and biting the air. If, as he is standing quietly, one foot be moved into a strained position, it is at once withdrawn and the uneasy pose corrected. When placed on a table, in the top of which there is a little trap-door so that one of his feet set on the trap can be let slowly down from under him, he allows the foot to sink a little way and then withdraws it smartly. One of the dogs in running about injured a hind-foot; after the hurt it still continued to roam on, but limping with three legs; that is, it was able to co-ordinate movements quite unusual to it. With these dogs when a light draught of air through a tube was turned upon the conjunctiva, the eye blinked and the head was turned aside. When the draught was directed to the ear the head was shaken. On the other hand, when the draught was turned upon the hair of the feet no notice was taken, although a normal dog will lift the foot at once and search for the disturbance.

The dog can feed itself, eating solid food, crunching bones and lapping up milk or water; but to start its feeding the muzzle has to be dipped into the dish. Food is not sought for, yet if feeding time be deferred the dog begins to show signs which seem to indicate impatience; he begins to move quickly about his cage, and rears himself against the bars, putting up his fore-paws on the railing. A little quinine (bitter) added to his sop of meat and milk led to the morsels, after being taken into the mouth, being without hesitation rejected. None were ever swallowed, although directly an undoctored piece was given it was swallowed and apparently with relish. Goltz threw to his own house-dog a piece of the same doctored meat. The creature wagged

his tail and took it greedily enough, then pulled a wry face and hesitated astonished; but he swallowed it. Perhaps he deemed it not seemly to appear ungrateful to the giver and reject the otherwise fair gift. He overcame his instinct and by his self-control gave proof of the intact cerebrum he possessed. A dog without cerebrum after the usual quantity of food has been taken invariably refuses to take more. The animal seems to know when appetite is appeased. As regards power of sight, the sudden flash of a bright light was evidently noticed, for the gaze was turned immediately in the direction of the light.

In spite of this high degree of motility and of reaction to sensory impressions, defects were also present to extremely marked extent. The patting, or stroking, or the offer of food, so pleasurable to a normal dog, and responded to so readily by a wag of the tail or other signs of friendship, elicited from the dog without cerebrum no reaction whatsoever, or, at most, a growl in reply to being touched. He paid no heed to the barking or the playful advances of his companions in the kennel. The whip held threateningly before him, though he could see it, did not make him cower. If after being washed he was left undried he shivered but did not attempt to shake or lick the water off himself. One dog which was under observation a year and a half never learned during all that time to remember that being lifted from the cage at noon was but a preliminary to his midday meal. He always struggled, resisting the removal and trying to bite the servant who lifted him and fed him. A normal dog after feeding usually licks the top of his nose once or twice, and if a piece of butter be stuck on the nose the dog, relishing the butter, will by repeated licking soon clear it all away. The dog without cerebrum after feeding invariably licked the top of its nose once or twice, as does a normal dog, and if butter were stuck on its nose the tongue, in licking the nose, got some of the butter, which was then swallowed apparently with relish, yet though much butter remained within reach on his own nose the creature never repeated the manœuvre

to obtain it. Further, it was noticeable that in feeding the fore-limbs, though used apparently so perfectly for progression, were never employed as by a normal dog to steady a bone being gnawed.

In some actions the dog without cerebrum returns to the instinct of the new-born puppy. Goltz writes that signs of anger and discomfort were frequently evinced, but never the slightest expression of any pleasure. Sleep was prolonged, but never broken by any signs of dreaming, such as are common within the normal dog.

It is clear that Goltz considers he is studying in the rest of the central nervous system after cerebrum is gone reactions linked to a sort of lower consciousness intermediate between "*rückenmarkseele*" and full consciousness of the whole system in integrity. He speaks of still existent, although blunted, sense of contact, vision, taste, etc. But it must be remembered that there are centripetal impressions which cause reactions unaccompanied by consciousness, and some of the so caused reactions are extremely complex. To one who studies the working of the central nervous system by experimentation upon lower animals the signalling code, through which he reads replies to his questions, rests almost solely on skeletal musculature. The motor reactions yielded by Goltz's dogs display a wealth, variety and complexity highly important to remember when applying such terms as "motor" "sensory" to the functions of the hemispheres. But how far were there with those reactions concomitant *σημεῖα*? How far were the diverse answers paralleled by changing states of consciousness? How far is it permissible to describe them in terms associated with sensation? *παράσσει τὸνς ἀνθρώπους οὐ τὰ πράγματα, ἀλλὰ τὰ περὶ τῶν πραγμάτων δόγματα.* The great complexity and co-ordination of function that still remain to the dog without cerebrum are perhaps well realised in comparing its condition with that of the patient anæsthetised in preparation for the surgeon's knife. The latter is unconscious, and it is evident to what a different depth the former has been plunged. The patient on the operation table cannot hear or see, still less get up and walk; when his eyeball is touched his lids do not reply;

though he breathes and his heart beats the muscles in his limbs lie slack; *amæba* has more of consciousness though less of nervous action. Between lowest and high nervous action stretches a realm which language, impotent to describe it, denominates baldly in three zones, *Empfindung*, *Wahrnehmung*, *Vorstellung*. This domain during recovery from chloroform is in the space of a few minutes reacquired, but its extent is vast. The reactions of the existences banished by Goltz to life-long wandering therein inform us of its nearly unknown scenery and give some measure of the huge monotony. The question arises, Which zone? Certainly not the ultimate.

How subtle the wealth of higher reactions lost and to how large a degree these lie obscured from our observation in the laboratory is taught by Goltz's work with unique force. The work emphasises further the relatively huge quantity of nerve-material engaged by elaboration of the crowning reactions.

In the dogs studied by Goltz not only the spinal cord and bulb but the cerebellum still remained. Those dogs are assuredly not too harshly entitled "imbecile". They lived devoid of memory, attention, and probably of all precision of sensation. It is not surprising then to find that from his observations on the results of extirpation of the cerebellum Luciani<sup>1</sup> should gather no evidence inferring in it the "highest level" reactions of the nervous system. Eight years of patient investigation lead him to connect this organ almost solely with muscular innervation, more especially with that proceeding *via* the so-called "motor region" of the opposite cerebral hemisphere.

He found that simple severance of the cerebellum into its two lateral halves produces barely any perceptible effect upon motility and none whatever on sensation. On the other hand lesions to either side the median longitudinal plane produce remarkable disorder. Thus after simple

<sup>1</sup> *Il Cervelletto*, Florence, November, 1891.

median section the gait, accurately studied by an ingenious device of the experimenter, after some temporary disturbance resembles in a few days the normal gait again. He noticed that though the consequences of destruction of one lateral half are severe, the further removal of the other half hardly at all aggravates the symptoms except to make their distribution bilaterally symmetrical instead of chiefly unilateral. Each half of the organ depends little on the other. After removal of one lateral half the dog wheels constantly toward the opposite side, and falls frequently, always toward the side homonymous with the lesion. Its movements are hindered on the homonymous side by want of power and steadiness in the contraction of the muscles. Luciani points out that the defective innervation of the muscles is so fundamentally different from that obtaining after ordinary spinal or cerebral damage that the terms paralysis and paresis employed for the latter are here undesirable, since likely to confuse, and he rejects them lest the appreciation of the profound difference be hindered. He therefore in his description, according as it relates to the tonus of resting muscles, and to the force, the steadiness and the mutual co-operation of contracting muscles, speaks of an *atonia*, an *asthenia* and an *astasia*,<sup>1</sup> as well as of the *ataxia* so well known. Cerebellar lesion induces all of these and chiefly on the homonymous side. Of the *asthenia* he obtained numerical measurements by ingenious employment of a dynamometer. After removal of one lateral half of the cerebellum the disuse of the limbs of the same side was in some animals so great that they might at first sight appear hemiplegic. In the dog the fore-limb became the more ataxic, the hind-limb the more asthenic. Tremor accompanied all muscular effort. The head shook when the recumbent animal looked up on being aroused. During progression the limbs and trunk muscles of the homonymous side trembled rhythmically. In the

<sup>1</sup> Luciani uses the word *astasia* with a different meaning than that given it by clinicians. He denotes by it want of steadiness of action in a muscle.

dog the prehensile precision of the neck is especially exercised in feeding from the dish on the cage floor, and it was then that oscillation of the head and neck became especially violent. Ablation of the limb region of the opposite cerebral hemisphere did not reduce but rather aggravated the tremor, as also the asthenia of the muscles.

Luciani notes as an important distinction between the disturbance due to ablation of the limb region of the cerebral cortex and that due to ablation of the cerebellum, that in the former there is great defect of tactile and muscular sensation of the limb, in the latter these are not obviously interfered with. "Basta toccare leggermente, in qualsiasi punto della cute, l'animale operato al cervelletto, mentre è intento a cibarsi, oppure mentre ha gli occhi bendati, perché esso, con qualche movimento reattivo, mostri subito di aver avvertito il contatto. Basta collocare in posizione incongrua l'uno o l'altro arto dell' animale, perché subito esso reagisca riponendo l'arto nella posa normale. In questo gli animali scerebellati si comportano in maniera affatto opposta a quelli privati di una porzione abbastanza cospicua delle *sfere sensorio-motrici* della corteccia cerebrale."

Yet the large command of motility residual in absence of even the whole cerebellum, and of the "*sfere sensorio-motrici*" of both cerebral hemispheres, is very evident in the history of a dog observed for a period of twelve months following on those ablations. The creature swam "a meraviglia," keeping its head up from the water in normal fashion, directing its course to right or left or straight forward at pleasure. Compensatory actions play a great part in gradually minimising the effects of the disturbance. Thus the insecurity of gait is minimised, as Luciani's tracings demonstrate, by the limbs being more widely spread and a wider base obtained for supporting the gravity of the body. After the "irritation symptoms" due to still active trauma have passed off, there is, Luciani believes, no real restoration of the actions that disappeared, though more or less compensation is obtained by means of other actions.

One of the chiefest functions of the cerebellum is, Luciani says, to exert by each of its own lateral halves on the so-called motor region (*sfera sensorio-motrice*) of the opposite cerebral hemisphere an influence comparable with the "bracing" action exerted by the centripetal stream which debouches from the sensory spinal nerve-root into the anterior cornu of the spinal cord, and maintains in the nerve-cells of the latter a steady gentle discharge into the skeletal muscles, the basis of the reflex muscular tone.

As to the details of the labour of the supreme hemispheres themselves, it may be said that Munk's researches in this subject last year reached a standpoint especially inviting retrospection. Of all the experimenters who early followed in the wake of Fritsch and Hitzig's<sup>1</sup> notable discovery, Munk,<sup>2</sup> with the exception of Hitzig's<sup>3</sup> himself, perhaps alone seized and described the phenomena in a way which has not since required fundamental modification, or indeed any modification at all further than that involved in the filling in of detail. He from the first (1877) described the cerebral cortex as a congeries of centres, whose spatial arrangement has sufficient differentiation to allow of their being grouped topographically in terms of sensory avenues by which each group lies easiest of access. Thus the *sehsphäre* or group of centres accessible *via* the optic nerve, the *hörsphäre* accessible *via* the auditory nerve, and so on. The *sphäre* is excitable not only indirectly, *e.g.*, *via* retina; stimuli applied to its intrinsic fibres are efficient and elicit for instance definite consensual movements of the eyeballs. Conversely in consequence of destruction of a *sphäre* specific sensory reactions, *e.g.*, those *via* retina, suffer damage or drop out entirely.

For Munk, as for its discoverer Hitzig, the parietal region of cortex whence can be elicited movement of the

<sup>1</sup> Du Bois-Reymond's *Archiv*, 1870.

<sup>2</sup> *Ibid.*, 1878.

<sup>3</sup> *Untersuchungen ueber das Gehirn*, Berlin, 1874.



limbs, neck, face, etc., resembles the *seh-* and *hörsphären*, differing from them in the locality and quality of the sensory surface with which connected rather than in the intrinsic quality of its own activity. To call those sensory and this motor is to imply between them a contradistinction which in the view of Munk does not exist. The cortical limb centre is one elaborated over sensory paths, not in its case paths from eye and ear but paths from skin and muscle and joint composing the limb itself. Just as the sensory reactions *via* retina suffer in consequence of sufficient damage of *sehspähre*, so those *via* the limb suffer in consequence of sufficient damage of the limb region, in what Munk calls the *gefühl-sphäre* of the cortex. Goltz,<sup>1</sup> obstinate opponent of Hitzig and Munk upon many points, so far was early at one with them and with Schiff,<sup>2</sup> in drawing attention to the blunted sensibility of the limb ensuing on destruction of the cortex cerebri. He measured the least weight which applied to the paw induced the dog to struggle to withdraw it. A weight of ten to sixteen on the defective side answered to one of four to six upon the sound; and this at a time when the dog had so far recovered from the ablation that "er lief und sprang wie ein gesunder Hund". The sensory end organs in the skin and musculature are to the *gefühl-sphäre* as those in the retina to the *sehspähre*. Just as motor reactions can be obtained in the eye muscles through the latter, so through the former motor reactions in the skeletal musculature; these latter had indeed been discovered altogether prior to Munk's work.

Each limb area in the *gefühl-sphäre* lies in especially close touch with motor nuclei for those very parts whence spring the sensory impressions playing upon the area itself. How greatly its sensory ingoings affect its motor outgoings is well seen in the experiments by Bubnoff and Heidenhain.<sup>3</sup> Thus; a stimulus of carefully selected strength is applied to

<sup>1</sup> Pflüger's *Archiv*, 1876, p. 9.

<sup>2</sup> *Archiv f. Exper. Pathol.*, 1875, p. 176.

<sup>3</sup> Pflüger's *Archiv*, 1881, p. 164.

a point of cerebral cortex connected with movement of one of the fore-paws. The strength of stimulus chosen is one just insufficient to evoke the movement. By stroking gently the skin of the paw itself the inefficient excitation is made at once efficient. Again; cortical excitation eliciting from the limb muscles a contraction of definite latency, this latency is increased two or three-fold by simultaneous excitation of sensory fibres from the limb itself. These easily-affected centres in the parietal cortex are, so to say, threaded upon extensions of the neuro-muscular circuits of Charles Bell (or the diastaltic arcs of Marshall Hall). The remarkable extent of spatial differentiation of these extensions of the circuits was early demonstrated by Ferrier (1873). The connection of the cortex with the neuro-muscular circuits even with the skeletal is however far from being equal for them all. Munk has insisted on three main grades of tie to be distinguished. Between the cortex and some of the circuits he doubts the existence of any tie at all. On the other hand, Hughlings Jackson has argued for connection between cortex and each and every circuit—of course not equal intimacy of connection. The movements damaged most by destruction of the cortex cerebri are movements fine in kind, such as those performed by the fingers and the thumb. Of such movements some are after extensive injury to the *gefühl-sphäre* never again executed. But coarser movements such as those at hip and shoulder suffer a slight derangement which is temporary.

Munk suggests that this difference is due to the finer movements being worked through cortical centres acting across subcortical, the latter of themselves sufficient for coarser co-ordinations such as those at the shoulder, etc. Against this suggestion is the known directness of tie between the cortical cells and the segmental spinal centres *via* pyramidal tract. The cortical centres are no doubt connected with countless cerebral subcortical, but yet we must think that in the execution of fine movements the former supervise the centres of lowest level directly, not indirectly. In estimating degree of impairment of move-

ment in a limb it must be remembered that defect is easier found in the fine apical parts than in the larger, coarser proximal. When Dr. Grace, the cricketer, drives two successive balls to the off, an inch less or more in the lunge forward of the shoulder is probably imperceptible to veteran players in the field, but the variation by a small fraction of an inch in the turn of the wrist is obvious at once to the least practised onlooker; the ball in consequence takes different direction between the surrounding fielders. The impairment of movement so obvious at the distal joints of the limb may exist at proximal also but be undetected. It is precision of movement of limb rather than apical movement of limb that suffers. Because in the motion of apical parts of the limb the *rôle* played by precision is greater than in proximal, apical movement appears so much injured.

In result of lesion of the *gefühl-sphäre* one derangement—a corollary naturally consequent in the view held by Munk—is very clearly exhibited by the interesting records recently published by Mott.<sup>1</sup> Mott notes that the impairment of cutaneous sensation is greater at the apex of the limb than in the proximal part of it. Were the muscular sense examined in suitable patients carefully as for normal persons by Goldscheider and Waller, it would probably reveal increasing deficit in a centrifugal direction along the serial portions of the limb. To make further comparison between limb cortex and visual cortex one might say that the apex of the limb in the former is the analogue of *fovea centralis* in the latter. Just as in the former the reactions of the digits predominate, so in the latter the reactions belonging to the fovea. The cortical projection of the thumb, as of the fovea, is relatively large. By such comparison becomes clearer the peculiar importance of the cerebral cortex for the “high level” movements, which find expression chiefly through the instruments of precision, the apical members of the limb. It is the reactions of these members which will suffer in the limb as in the retina the reactions of the region of central

<sup>1</sup> *Journal of Physiology*, January, 1894, p. 464.

vision. Among centripetal impressions streaming in from the limb, as from the retina, are many unaccompanied by parallel subjective process, and many more accompanied by only dim subjective states, but over and above these the cortex sits at receipt of those specific perceptions (*wahrnehmungen*) whence the fully elaborated "mental pictures of the moment" (*vorstellungen*). Therefore does its absence involve defect in accuracy of sensation and of movement.

In describing the impairment of the apical movements of the limb Munk points out that though normally the apical movements are elicitable both individually and as parts of sequences, after destruction of the "limb cortex" movement of a thumb or finger is no longer elicitable individually, but only as part of a sequence; the sequence, he says, then runs always from proximal to distal joints, *i.e.*, a "centrifugal radial sequence," to follow Mercier.<sup>1</sup>

Concerning restoration of function after structural injury to the central nervous system, Munk, like Goltz, rejects the possibility that recovery from paresis of cortical origin is explicable by assumption or extension of correlative functions seated in the cortex of the opposite hemisphere. Both observers lay stress on the suppression of defects under occasions of mental excitement and activity. The paretic dog as feeding-time approaches becomes less paretic (Goltz);<sup>2</sup> his field of vision reduced by occipital lesion becomes less so (Loeb);<sup>3</sup> "Leidenschaftlich erregt, in Angst und Furcht oder gierig nach der Nahrung, läuft der Affe oder geht er rasch; und dann werden schon zu derselben Zeit, zu welcher beim gewöhnlichen langsamen Gehen, das wir vorhin verfolgten, die unteren Glieder der rechten Extremitäten noch passiv geschleift werden und der Affe öfters umfällt, alle Glieder der rechten Extremitäten activ derart bewegt, dass der Affe ohne zu stolpern oder zu fallen,

<sup>1</sup> *The Nervous System and the Mind*, London, 1888.

<sup>2</sup> *Pflüger's Archiv*, 1883.

<sup>3</sup> *Ibid.*, 1884, vol. xxxiv., p. 67.

schön vorwärts kommt" (Munk).<sup>1</sup> The cortex may thus be likened to a black hot ember which under the breath of "attention" is made to glow at one point or another; but, not only may the oxygen stream upon it be now more now less, there affect it also seasons of intrinsic excitement, when the same stimulus will make it glow more fiercely than at others. Ruins of cell groups and miserable paucities of fibres, insufficient to awake or propagate reactions under ordinary circumstances, then become sufficient. Of similar origin may be the temporary improvements that often mercifully break the monotony of a relentlessly progressive, at least never really regressive, chronic nerve-disease. The condition is akin to, though it includes more than, mere increase of "suggestibility": normal barriers become strengthened as well as ways more easy.

Among the disturbances caused by cerebral injury a part pass rapidly away. These "hemmungerscheinungen" or inhibitions are due to irritation radiating from the seat of trauma. With modern aseptic traumata these irritative disturbances can hardly last more than a few days. The rôle ascribed to them has probably been exaggerated. The amount of true return of function has probably also been over-estimated. Improvement of symptoms need not mean return of actions. The shoemaker, who after Rolandic lesion lost power in the hand, and was unable to pick up his awl betwixt the thumb and index, after a time, though still unable with the thumb and *index*, effected the same thing with the thumb and *medius*.<sup>2</sup> Such compensatory actions attain the original object by circuitous route. They serve, according to Luciani, in manifold instances to alleviate the trouble after cerebellar ablations. Real restitution of the original action seems little possible. The cells of the nervous system are laid down in certain quantity at an early epoch of embryonic life and unlike many in the body are "without power to add to their number". Numerically their installation is from an early date complete. Removed

<sup>1</sup> *Sitzungb. d. k. pr. Akad. d. Wiss. Z. Berlin*, xxxix., p. 2.

<sup>2</sup> R. Lépine, *Rev. Mensuelle de Médec. et de Chirurgie*, 1880, p. 765.

or destroyed there is no reproduction of more. Their number is fixed, but individually they possess enormous power of growth, developing through a long period (probably far on into adult life of the organism) both in complexity and size. The length of some of the slowly grown cell branches is more suitably measured by feet instead of the thousandths of a millimetre used with other cells. They are also remarkable for their length of individual life; in a centenarian we may consider his nerve-cells have led unbroken individual existences for more than a hundred years, though many within that time have probably reached their span and quietly "run down".

But though unable to produce new cells the nerve-cell is able to reproduce its own branches when they have been torn through or otherwise destroyed. Like the bits into which Verworn<sup>1</sup> tore up the Radiolarian, the cell portions containing no nucleus enter slow degeneration and die (Wallerian degeneration); but that containing the nucleus repairs itself and reforms a perfect cell. It grows its processes again and with a tolerable accuracy. If education is related to the throwing out of new "dendrons" and "collaterals" by nerve-cells,<sup>2</sup> some cells for the greater part of life retain a power not merely to repair a cell branch but to put forth new twigs. If so, a part of the mysterious restoration of function following destructive lesions of the nervous system may perhaps be due to actually new structural connections. The existing nerve-cells may not merely restore some of the old lines where broken, but push out communications altogether new. Fresh combinations thus obtained may lower or heighten pre-existing resistances and will at least partially rearrange them.

Even these brief annotations will have sufficed to indicate how difficult at present to describe the reactions of the cortical regions, without in the description

<sup>1</sup> Pflüger's *Archiv*, vol. li., p. 1, 1892.

<sup>2</sup> *Ramon-y-Cajal Nuevo conceptod. l. Histol. d. l. Centros Nerviosos*, Barcelona, 1893.

implying too much or indicating too little. Authorities who represent in some respects the poles of opinion on cerebral physiology, nevertheless agree in deprecating altogether such nomenclature as "motor cortex," "sensory cortex". The view no doubt in the minds of all has been that of a "through" station, "diastaltic" to use the old terminology; but some in laying stress on the outcome (on the "expressions" as Waller says) have briefly used the word "motor" (Ferrier), while others laying stress on the ingoings (the "impressions") have briefly written "sensory" (Schiff). For all this difficult aspect of the subject, and indeed for many others, the reader should turn to the lucid essay by Waller,<sup>1</sup> a critical exposition of the whole matter and the best. In concluding here the brief notice of Munk's experimental observations and teaching it must however be remarked that, believing the occipital, the temporosphenoidal and the Rolandic regions of the cortex to be of co-equal physiological valency, he unlike many does not exclude from the Rolandic region the "seat of consciousness".

An interesting point, which it would be especially interesting to hear Munk discuss, though nowhere so far as I know does he allude to it, is the long difference of latency discovered by Schäfer<sup>2</sup> to exist between the reaction upon the same muscles as obtained from the occipital or from the parietal regions, both according to Munk on the same physiological level.

It is notable that the activity of reactions involving the cortex, if we examine them in measure of sensation (so far as that is possible, *i.e.*, by least observable difference between two sensations), increases most rapidly for stimuli nearest to liminal intensity. If, taking Munk's view of the Rolandic cortex, we then assume the Weber-Fechner law holds also true for its centrifugal discharges, these, even if forwarded still in obedience with the law by spinal cells, will when arriving at muscle evoke, to judge by the curve

<sup>1</sup> *Brain*, p. 329, 1892.

<sup>2</sup> *International Journal of Anatomy and Physiology*, 1888, vol. v., pt. iv.



recently obtained by Cybulski and Zanietowski,<sup>1</sup> contraction following a quite different curve of ratio. We can never therefore expect for reactions obtained *via* the cortical centres that the quantities of muscular work resulting out of them (the very quantities most accessible to measurement) will bear a ratio to stimulus expressible by the well-known logarithmic curve.

C. S. SHERRINGTON.

<sup>1</sup> Pflüger's *Archiv*, vol. lvi., p. 45.